SHOUT
SHARE
IT

SBM
1020

BULLETIN OF
THE BRITISH MUSEUM
(NATURAL HISTORY)

BRITISH MUSEUM
11 SEP 1970
NATURAL HISTORY

GEOLOGY
VOL. XV
1967–1968

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)
LONDON: 1970

DATES OF PUBLICATION OF THE PARTS

No. 1.	26th May	1967
No. 2.	13th June	1967
No. 3.	24th November	1967
No. 4.	12th January	1968
No. 5.	19th March	1968
No. 6.	14th May	1968

PRINTED IN GREAT BRITAIN
BY ALDEN & MOWBRAY LTD
AT THE ALDEN PRESS, OXFORD

CONTENTS

GEOLOGY VOLUME XV

No. 1. The palaeontology and stratigraphy of the lower part of the Upper Kimmeridge Clay of Dorset. J. C. W. Cope 1

No. 2. The correlation and trilobite fauna of the Bedinan Formation (Ordovician) in south-eastern Turkey. W. T. Dean 81

No. 3. Burrows and surface traces from the Lower Chalk of southern England. W. J. Kennedy 125

No. 4. A new *Tempskya* from Kent. M. E. J. Chandler 169

No. 5. Colonial Phillipsastraeidae from the Devonian of south-east Devon, England. C. T. Scrutton 181

No. 6. Some Strophomenacean brachiopods from the British Lower Silurian. L. R. M. Cocks 283

Index to Volume XV 325

25 MAY 1967
NATURAL HISTORY

THE PALAEONTOLOGY AND STRATIGRAPHY OF THE LOWER PART OF THE UPPER KIMMERIDGE CLAY OF DORSET

J. C. W. COPE

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 1
LONDON: 1967

25 MAY 195
NATURAL HIST

THE PALAEONTOLOGY AND STRATIGRAPHY OF THE LOWER PART OF THE UPPER KIMMERIDGE CLAY OF DORSET

BY

J. C. W. COPE
Department of Geology, University College, Swansea

Pp. 1–79; 33 *Plates;* 12 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 1
LONDON: 1967

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 15, *No.* 1 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

© Trustees of the British Museum (Natural History) 1967

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 26 *May*, 1967 *Price* £4 15*s*.

THE PALAEONTOLOGY AND STRATIGRAPHY OF THE LOWER PART OF THE UPPER KIMMERIDGE CLAY OF DORSET

By J. C. W. COPE

CONTENTS

Page

I. INTRODUCTION 4
II. THE KIMMERIDGE SECTION 5
III. THE NON-AMMONITE FAUNA 10
IV. THE AMMONITE FAUNA 11
  (a) INTRODUCTION 11
  (b) SYSTEMATIC DESCRIPTIONS 12
    Genus *Gravesia* Salfeld 12
      Gravesia gigas (Zieten) 12
      G. cf. *gravesiana* (d'Orbigny) 14
    Genus *Pectinatites* Buckman 14
      Sexual Dimorphism 15
      Interpretation of *Pectinatites* 18
      The Origins of *Pectinatites* 22
    Subgenus *Arkellites* nov. 24
      Pectinatites (*Arkellites*) *primitivus* sp. nov. 24
      P. (*A.*) *cuddlensis* sp. nov. 26
      P. (*A.*) *damoni* sp. nov. 28
      P. (*A.*) *hudlestoni* sp. nov. 29
    Subgenus *Virgatosphinctoides* Neaverson 30
      Pectinatites (*Virgatosphinctoides*) *elegans* sp. nov. . . 31
      P. (*V.*) *elegans corniger* subsp. nov. 33
      P. (*V.*) *scitulus* sp. nov. 34
      P. (*V.*) *decorosus* sp. nov. 36
      P. (*V.*) *major* sp. nov. 37
      P. (*V.*) *clavelli* sp. nov. 39
      P. (*V.*) *smedmorensis* sp. nov. 41
      P. (*V.*) *laticostatus* sp. nov. 43
      P. (*V.*) *grandis* (Neaverson) 44
      P. (*V.*) *grandis acceleratus* subsp. nov. 45
      P. (*V.*) *woodwardi* (Neaverson) 45
      P. (*V.*) *wheatleyensis* (Neaverson) 46
      P. (*V.*) *wheatleyensis minor* subsp. nov. 47
      P. (*V.*) *wheatleyensis delicatulus* (Neaverson) . . . 48
      P. (*V.*) *pseudoscruposus* (Spath) 49
      P. (*V.*) *reisiformis* sp. nov. 50
      P. (*V.*) *reisiformis densicostatus* subsp. nov. . . . 53
      P. (*V.*) *abbreviatus* sp. nov. 54
      P. (*V.*) *donovani* sp. nov. 55
      P. (*V.*) *magnimasculus* sp. nov. 56
      P. (*V.*) *encombensis* sp. nov. 57

Page
Subgenus *Pectinatites* Buckman 59
Pectinatites (*Pectinatites*) *inconsuetus* sp. nov. . . 59
P. (*P.*) *eastlecottensis* (Salfeld) 60
P. (*P.*) cf. *groenlandicus* (Spath) 61
P. (*P.*) *cornutifer* (Buckman) 62
P. (*P.*) *naso* (Buckman) 62
Genus *Pavlovia* Ilovaisky, subgenus *Paravirgatites* Buckman 63
Pavlovia (*Paravirgatites*) cf. *paravirgatus* (Buckman) . 63
V. EVOLUTION OF THE AMMONITES 64
VI. THE AMMONITE ZONES 66
Pectinatites (*Virgatosphinctoides*) *elegans* Zone . . 66
P. (*V.*) *scitulus* Zone 68
P. (*V.*) *wheatleyensis* Zone 69
P. (*Arkellites*) *hudlestoni* Zone 69
P. (*Pectinatites*) *pectinatus* Zone 70
VII. CORRELATIONS 70
(a) Great Britain 70
(b) The Boulonnais 72
(c) East Greenland (Milne Land) 73
(d) Southern Germany (Franconia) 73
(e) Russia (Basin of the Ural and Ilek Rivers) 75
VIII. REFERENCES 76

SYNOPSIS

Re-examination of the lower part of the Upper Kimmeridge Clay of the type section at Kimmeridge, Dorset, has involved detailed collecting and re-measurement of the succession. The ammonite fauna of some 465 ft. of these beds is described.

The ammonites belong to three subfamilies; three genera are represented, and descriptions are given of three subgenera (one new); twenty-eight species (seventeen new); and five subspecies (four of them new).

Sexual dimorphism is recognized in one genus, and is believed to be of a unique type.

A revised zonal scheme is proposed, and correlations are suggested with Northern France, Greenland, and other areas of Britain.

Comparisons are made with the ammonite fauna of other extra-British areas. The fauna of the Lower Tithonian rocks of Germany is shown to be quite distinct from that of the Upper Kimmeridgian of Britain, such similarities as exist being entirely due to homeomorphy.

I. INTRODUCTION

EXISTING knowledge of the Upper Kimmeridgian ammonite faunas of Britain is very imperfect. The research work which forms the basis of this account is the first stage of a planned research project, in the course of which it is proposed to study these rocks and their faunas over the whole of Britain.

The lower Kimmeridgian fauna of Britain is comparatively well known and it was, therefore, considered that the best way to carry out this work was to begin at the base of the Upper Kimmeridgian (the base of the present *Gravesia* Zones) and work upwards to the Portlandian.[1] The scope of the first part of the work embraces the *Gravesia*, " *Subplanites* " and basal *Pectinatites* Zones of the type-section.

---

[1] The Middle Kimmeridgian of Arkell (1956 : 21) has, as a result of the conclusions presented herein, no real standing. It seems most appropriate to have, therefore, two subdivisions of the Kimmeridgian Stage, the line between them being drawn at the top of the *Aulacostephanus autissiodorensis* Zone.

Prior to 1913 most of the ammonites from the British Upper Kimmeridgian were known under the name of *Ammonites biplex*—a name which embraced practically all Upper Jurassic perisphinctid ammonites.

In 1913 Salfeld identified some of the British Upper Kimmeridgian ammonites with Pavlow's genus *Virgatites*. Neaverson (1925) showed that these ammonites were not related to the Russian Volgian forms as Salfeld had supposed. Neaverson's work, valuable though it was, fell far short of monographing the whole ammonite fauna from these beds. Neaverson did not undertake comprehensive collecting from the type-section in Dorset, which surely must be the basis for zonal subdivision. The sequence there is a thick one, and as far as is known, complete. In contrast, the sections in the Oxford district, taken by Neaverson as the basis for his zonal scheme, are incomplete and very much attenuated. As a result, parts of his zonal scheme are unsatisfactory.

Spath in the early 1930's made a collection from the Kimmeridge section (now housed in the British Museum (Natural History)), and although this was never described, references are made to it in several of his papers (e.g. 1935 : 73). He identified Neaverson's genera *Allovirgatites* and *Virgatosphinctoides* with his genus *Subplanites*, proposed in 1925 for a group of ammonites occurring in Franconia; he later identified other British forms with the Tithonian genus *Lithacoceras*; and as a result, correlations became established between Britain and Germany based on these genera. These correlations were followed among others by Arkell (1956), and have now become generally accepted.

The collections from Dorset now to be described, however, establish beyond doubt that the British Upper Kimmeridgian and German Tithonian forms are not identical, and these previous correlations are thus without real value.

Many colleagues and friends have been of invaluable assistance in providing helpful suggestions and criticisms. I am particularly indebted in this respect to Professor D. T. Donovan, Dr. J. H. Callomon, and Dr. A. Zeiss.

The receipt of a Research Studentship from the former Department of Scientific and Industrial Research, a grant from the British Council under the Younger Research Workers Interchange Scheme, and financial assistance from the University College of Swansea are gratefully acknowledged.

II. THE KIMMERIDGE SECTION

The Kimmeridge Clay is the oldest formation exposed on the Isle of Purbeck. It appears as a long strip, approximately six miles in length and usually less than a mile wide, in the core of the Purbeck Anticline. To the north the steep escarpment of the Portland Stone effectively isolates this relatively low-lying land. The village of Kimmeridge is situated in a hollow beneath this escarpment.

The outcrop of the Kimmeridge Clay on the northern limb of the Purbeck Anticline occurs in a military zone extending five miles westwards from Kimmeridge, and is for this reason inaccessible. Eastwards from Kimmeridge Bay, however, the section is well displayed for over three miles on the southern limb of the anticline. The sea erodes at a substantial rate the relatively soft shales which comprise the bulk of the succession, but has little effect on the occasional cementstone bands which stretch out from the base of the cliffs to form the Kimmeridge Ledges, presenting a considerable hazard to shipping.

The cliffs, which are seldom more than 150 ft. in height, are precipitous and crumbling. A constant trickle of shale debris down the cliffs builds up piles of talus at their foot. Occasional larger falls bring down large pieces of the cementstone bands which litter the shore at the cliff base, and break the force of the waves. It is generally only at high spring tides that the sea can reach the foot of the cliffs.

At the foot of the beach at low tide small ledges or reefs of shale are exposed, and these are the only places where fossils can be satisfactorily collected.

The part of the Kimmeridge section described herein embraces parts of the Kim-

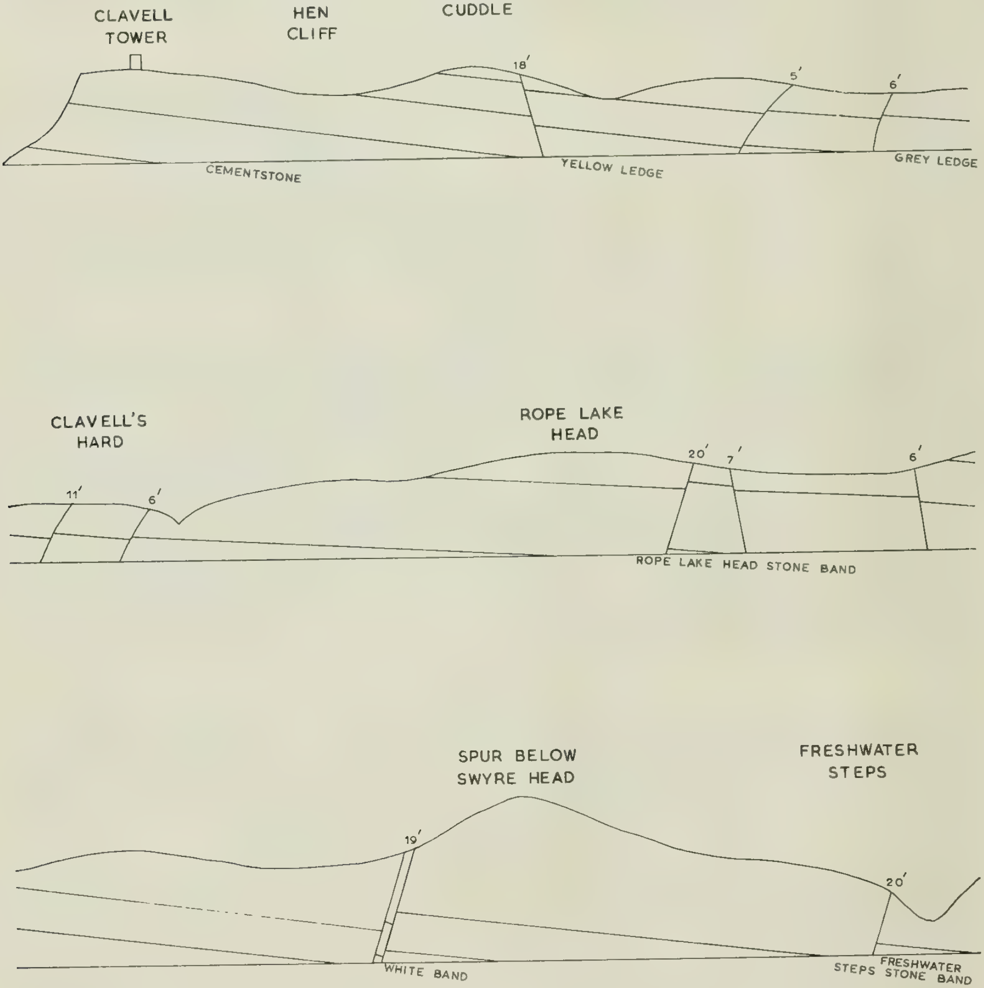

CLAVELL TOWER
HEN CLIFF
CUDDLE
18'
5'
6'
CEMENTSTONE
YELLOW LEDGE
GREY LEDGE
CLAVELL'S HARD
ROPE LAKE HEAD
11'
6'
20'
7'
6'
ROPE LAKE HEAD STONE BAND
SPUR BELOW SWYRE HEAD
FRESHWATER STEPS
19'
20'
WHITE BAND
STEPS
FRESHWATER STONE BAND

FIG. 1. Section of the cliffs from the eastern end of Kimmeridge Bay to Freshwater Steps. Modified after Arkell 1947 : 75.

meridge Clay, whose faunas have hitherto been very imperfectly known. The lowest horizon from which collections have been made is the cementstone band which forms a prominent reef on the foreshore at the western end of Hen Cliff. This bed marks, in the Kimmeridge section, the top of the *Aulacostephanus autissiodorensis* Zone, and therefore forms the junction between the Lower and Upper Kimmeridge Clay. The highest horizon studied is some twenty feet above the Freshwater Steps Stone Band. It is proposed to describe, at a later date, the highest beds of the Kimmeridge Clay, lying above this latter horizon and upwards to the Portlandian rocks.

This section has been re-measured in detail, using direct measurement where possible, supplemented by data acquired using an Abney level to measure the thicker lithological units, and to fix the position of the shale ledges relative to the nearest marker horizon.

The system of bed numbering used is that of Blake (1875 : 198–199) who was the first to make a detailed description of this section. Although Blake numbered his beds from the top downwards (thus Bed 1 was the last to be deposited), his bed numbers are for the most part well-defined. It was found that Blake's measurements were substantially correct, but there are several quite considerable errors, some being perpetuated by Arkell (1947 : 71–72).

In the description given below, only major lithological units are described. The stratigraphical range of a species may be found more accurately by reference to the systematic description of the species, or the section on the zonal stratigraphy.

Blake's Bed Number		*ft.*	*in.*
	***Pectinatites* (*Pectinatites*) *pectinatus* Zone**		
9	Shales *Pectinatites* (*Pectinatites*) *naso*, *P.* (*P.*) *cornutifer*, *Pavlovia* (*Paravirgatites*) *paravirgatus*, *Ostrea bononiae*, *Discina latissima*.	20	0
10	Freshwater Steps Stone Band	1	3
11	Shales *Pectinatites* (*Pectinatites*) *cornutifer*, *P.* (*P.*) *groenlandicus*, *P.* (*P.*) *eastlecottensis*, *P.* (*P.*) *inconsuetus*, *Ostrea bononiae*, *O. solitaria*, *Protocardia morinica*, *Discina latissima*.	29	0
12 pars	Middle White Stone Band	1	6
12 pars–20 pars	Shales and mudstones *Pectinatites* (*Pectinatites*) cf. *eastlecottensis*, *P.* (?*Arkellites*) sp. indet., *Ostrea* sp.	29	4
20 pars	White Stone Band	3	0

Blake's Bed Number		ft.	in.
	Pectinatites (Arkellites) hudlestoni Zone		
20 pars –23	Shales, mudstones, hard " dicey " bands	51	8
	Pectinatites (*Virgatosphinctoides*) *encombensis*, *P.* (*V.*) *magnimasculus*, *P.* (*Arkellites*) *hudlestoni*, *Lucina miniscula*, *Protocardia morinica*, *Ostrea bononiae*, *Discina latissima*, *Ichthyosaurus* sp.		
24	Basalt Stone Band	3	10
	Inoceramus expansus, *Ostrea* sp.		
25	"Dicey" mudstones	55	0
	Pectinatites (*Virgatosphinctoides*) *donovani*, *Inoceramus expansus*, *Parallelodon* sp.		
26 pars	Shales	13	1
	Pectinatites (*Arkellites*) *hudlestoni*, *P.* (*Virgatosphinctoides*) *reisiformis*, *P.* (*V.*) *reisiformis densicostatus*, *P.* (*V.*) cf. *reisiformis*, *P.* (*V.*) *abbreviatus*, *P.* (*V.*) *grandis acceleratus*, *Ostrea bononiae*, *Ostrea multiformis*, *Ostrea* sp., *Protocardia* sp., *Discina latissima.*		
26 pars	Cementstone		4
26 pars	Shales	8	11
	Pectinatites (*Virgatosphinctoides*) *reisiformis*, *Ostrea bononiae*, *Ostrea* sp.		
26 pars	Rope Lake Head Stone Band	1	6
	Pectinatites* (*Virgatosphinctoides*) *wheatleyensis Zone		
26 pars	Shales	14	7
	Pectinatites (*Virgatosphinctoides*) *reisiformis*, *P.* (*V.*) *wheatleyensis delicatulus*, *P.* spp. indet., *Ostrea* sp.		
26 pars	The Blackstone, or Kimmeridge Oil Shale	2	10
	Pectinatites (*Virgatosphinctoides*) *wheatleyensis delicatulus*, *P.* spp. indet, *Saccocoma* sp., *Ostrea* sp., *Discina latissima*, *Lepidotus* sp.		
27 pars	Shales	13	6
	Pectinatites (*Virgatosphinctoides*) *wheatleyensis*, *P.* (*V.*) *wheatleyensis delicatulus*, *P.* (*V.*) *grandis*, *P.* (*V.*) *pseudoscruposus*, *P.* (*V.*) cf. *pseudoscruposus*, *P.* (*V.*) *laticostatus*, *P.* (*V.*) *woodwardi*, *Saccocoma* sp., *Ostrea bononiae*, *Protocardia morinica*, *Lucina miniscula*, *Discina latissima*, *Lingula ovalis*, *Cerithium* sp.		
27 pars	Siltstone		1
27 pars	Shales	2	3
	Pectinatites (*Virgatosphinctoides*) *laticostatus*, *P.* (*V.*) *woodwardi*, *P.* (*V.*) *wheatleyensis*, *P.* (*V.*) *grandis*.		

Blake's Bed Number		*ft.*	*in.*
27 pars	Siltstone *Pectinatites* (*Virgatosphinctoides*) *laticostatus*, *Discina latissima.*		1
27 pars	Shales *Pectinatites* (*Virgatosphinctoides*) *grandis*, *P.* (*V.*) *wheatleyensis minor*, *Ostrea* sp.	1	10
28–30	"Dicey" mudstones and shales *Pectinatites* (*Virgatosphinctoides*) *laticostatus*, *P.* (*V.*) *smedmorensis*, *P.* (*V.*) *clavelli*, *Ostrea bononiae*, *Protocardia morinica*, *Lingula ovalis.*	45	5
31	Grey Ledge Stone Band (Top Ledge of Spath)	2	3

***Pectinatites* (*Virgatosphinctoides*) *scitulus* Zone**

Blake's Bed Number		*ft.*	*in.*
32–33	Upper Cattle Ledge Shales		
32	"Dicey" mudstones *Ostrea* sp.	18	5
33	Shales *Ophthalmosaurus* sp.	17	5
34	Cattle Ledge Stone Band *Pectinatites* (*Virgatosphinctoides*) cf. *major.*	1	8
35	Lower Cattle Ledge Shales *Pectinatites* (*Virgatosphinctoides*) *scitulus*, *P.* (*V.*) cf. *scitulus*, *P.* (*V.*) *decorosus*, *P.* (*V.*) *major*, *P.* (*V.*) cf. *major*, *P.* (*Arkellites*) *cuddlensis*, *P.* (*A.*) *damoni*, *Gravesia* cf. *gravesiana*, *Ostrea bononiae*, *O. multiformis*, *Protocardia morinica*, *Lucina miniscula*, *Modiola autissiodorensis*, *Exogyra virgula*, *Lingula ovalis*, *Discina latissima*, *Cerithium* sp., *Pliosaurus* sp., *Thrissops* sp.	51	5
36	Yellow Ledge Stone Band *Pectinatites* (*Arkellites*) *cuddlensis*, *P.* (*Virgatosphinctoides*) *elegans corniger*, *P.* (*V.*) cf. *scitulus.*	1	6

***Pectinatites* (*Virgatosphinctoides*) *elegans* Zone**

Blake's Bed Number		*ft.*	*in.*
37– 41 pars	Hen Cliff Shales *Pectinatites* (*Virgatosphinctoides*) *elegans*, *P.* (*V.*) *elegans corniger*, *P.* (*V.*) *major*, *P.* (*V.*) cf. *major*, *P.* (*Arkellites*) *cuddlensis*, *P.* (*A.*) *primitivus*, *P.* sp. indet., *Gravesia gigas*, *G.* cf. *gravesiana*, *Ostrea bononiae*, *Ostrea multiformis*, *Ostrea* sp., *Exogyra virgula*, *Trigonia pellati*, *Protocardia morinica*, *Lucina miniscula*, *Modiola autissiodorensis*, *Lingula ovalis.*	69	3

Blake's Bed Number		ft.	in.
41 pars	Cementstone	1	0
41 pars	Shale	1	11
	Pectinatites (*Arkellites*) cf. *primitivus*.		
42	Cementstone		8
	Pectinatites (*Arkellites*) cf. *primitivus*.		
	TOTAL THICKNESS	464	6

III. THE NON-AMMONITE FAUNA

The non-ammonite fauna, although often abundant in terms of individuals, is represented by few species.

VERTEBRATA

PISCES. Fish remains are common throughout the succession, but consist mainly of isolated scales. Fish scales are exceedingly abundant in the Pectinatus Zone. Identifiable fish remains include *Thrissops* sp., and *Lepidotus* sp.

REPTILIA. Vertebrae and occasionally other bones occur quite commonly. The anterior part of a skeleton of *Ophthalmosaurus* was found 12 ft. above the Cattle Ledge Stone Band, and a skull of *Ichthyosaurus* from 12 ft. below the White Stone Band. A posterior tooth of a Pliosaur was found 5 ft. above the Yellow Ledge Stone Band.

BRACHIOPODA

Discina latissima (Sow.) occurs throughout, but is more common above the Blackstone Band.

Lingula ovalis Sow. also ranges through the succession, but appears to reach its maximum just above the Yellow Ledge Stone Band.

ECHINODERMATA

One species of crinoid (*Saccocoma* sp.) occurs as isolated pyritized plates. It appears to be confined to the Blackstone and the ten feet of shale immediately below.

MOLLUSCA

GASTROPODA: Species of *Cerithium* have been found 27 ft. above the Yellow Ledge Stone Band, and 3 ft. below the Blackstone; apart from these occurrences no other gastropods were recorded.

BIVALVIA: Bivalves are the most abundant of the non-ammonite fauna. *Exogyra virgula* (Defrance) occurs up to 27 ft. above the Yellow Ledge Stone Band.

Protocardia morinica (de Loriol) and *Lucina miniscula* Blake are abundant throughout.

Ostrea bononiae Sauvage and *O. multiformis* Koch & Dunker, commonly occur attached to the undersurfaces of ammonite shells.

Other bivalves include *Trigonia pellati* Mun-Chal., *Parallelodon* sp., *Inoceramus expansus* Blake, *Ostrea solitaria* Sow., and *Modiola autissiodorensis* (Cott.)

Nautiloids and belemnites are absent from the fauna.

IV. THE AMMONITE FAUNA

(a) Introduction

The state of preservation of the ammonites from the Kimmeridge section leaves much to be desired from the point of view of palaeontological investigations.

The nodule bed in the Rotundum Zone of the Kimmeridge Clay is well known as one horizon which yields reasonably well preserved uncrushed ammonites. The author has found uncrushed, or relatively uncrushed, specimens at two other horizons, both of them in the part of the section described herein. One large isolated nodule 25 ft. below the Yellow Ledge Stone Band yielded a few pyritized ammonite nuclei, none of which are determinable specifically. The other horizon, the roof bed of the Blackstone, yields ammonites preserved in solid pyrite, but in which, unfortunately, the septa have been completely pyritized and have become destroyed.

All the other ammonites from other horizons have suffered crushing to a high degree. The ribbing, however, is generally well preserved, and is the basis for identification. The suture has almost invariably been completely obliterated.

Considerable problems have had to be surmounted both in the collection and the preparation of these ammonites. Fossils cannot be collected from the cliffs, owing to the fissile nature of most of the rock, and the consequent weathering of the shale along the bedding. The abundant pyrite has oxidized, and the resulting selenite crystals cover the surface of the bedding planes.

The shale reefs exposed at the base of the beach at low tide are the only places where ammonites can be satisfactorily collected.

At some horizons, because of the very closely-spaced joints in the mudstone bands, it is impossible to extract the ammonites. In this case a plaster cast of the ammonite impression is made in the field. The detail reproduceable with thinly-mixed plaster is excellent, and the casts so obtained are, for most purposes, as satisfactory to work with as the actual ammonites from other horizons.

The ammonites as they are extracted from the rock form most unpromising-looking material from the palaeontological point of view, and careful preparation is necessary before sufficient detail is visible for any determinative work.

The rib interspaces are filled with hard shale, and often the whole ammonite is encrusted with irregular pyrite aggregates. The lower surface of the ammonite (lower surface of the ammonite as it lies in the rock) is very often more or less encrusted with oysters which are impossible to remove successfully.

The crushing of the ammonites has affected most of the original measurements. The diameter has been increased by the flattening of the outer whorls; the whorl height is similarly affected, whilst the whorl thickness is reduced to about one-eighth of the original dimension. The diameter of the umbilicus is, however, relatively unchanged. The crushing of the outer whorl has the effect of making the point of bifurcation of the ribs appear much lower on the whorl side than it is in reality.

For purposes of identification and speciation, therefore, the conventional four measurements are not given (i.e. diameter, then the other three measurements expressed as a percentage of the diameter). Instead the diameter and the umbilical diameter only are given. These are both given as measurements since, as mentioned above, the diameter has been increased by the crushing.

Also given, where possible, are the number of primary and secondary ribs on the outer whorl, and the number of ribs at various diameters (usually at 5 mm. intervals) within the umbilicus.

In most cases the macroconch of a species is designated as the holotype. Where this is not possible (i.e. when the macroconch of a species has not been found, or when no well-preserved macroconch has been obtained), the microconch is designated as the holotype.

In cases where the collection of specimens can only be carried out by the making of plaster casts in the field, the macroconch casts have, not infrequently, very much obscured inner whorls. The reason for this is that the casts are made of the under-surface of the ammonites as they lie in the rock, and these under-surfaces are often encrusted with oysters.

(b) Systematic descriptions

Phylum Mollusca

Class *CEPHALOPODA*

Sub-class *AMMONOIDEA*

Order AMMONITIDA

Superfamily **PERISPHINCTACEAE**

Family **PERISPHINCTIDAE**

Sub-family **AULACOSTEPHANINAE** Spath 1924

Genus ***GRAVESIA*** Salfeld 1913

Type species by subsequent designation (Roman 1938): *Ammonites gravesianus* d'Orbigny 1850.

Gravesia gigas (Zieten)

(Pl. 1, fig. 1)

1830 *Ammonites gigas* Zieten, pl. 13, fig. 1.
1963 *Gravesia gigas* (Zieten); Hahn: 97, pl. 9, pl. 10, figs. 1, 2 (see also for earlier references).

Material. Two specimens.

Stratigraphical range. 40–45 ft. below the Yellow Ledge Stone Band.

Description. These two specimens, which are similar to one another, are crushed flat. Diameter 308–322 mm. Diameter of umbilicus 104–114 mm. The

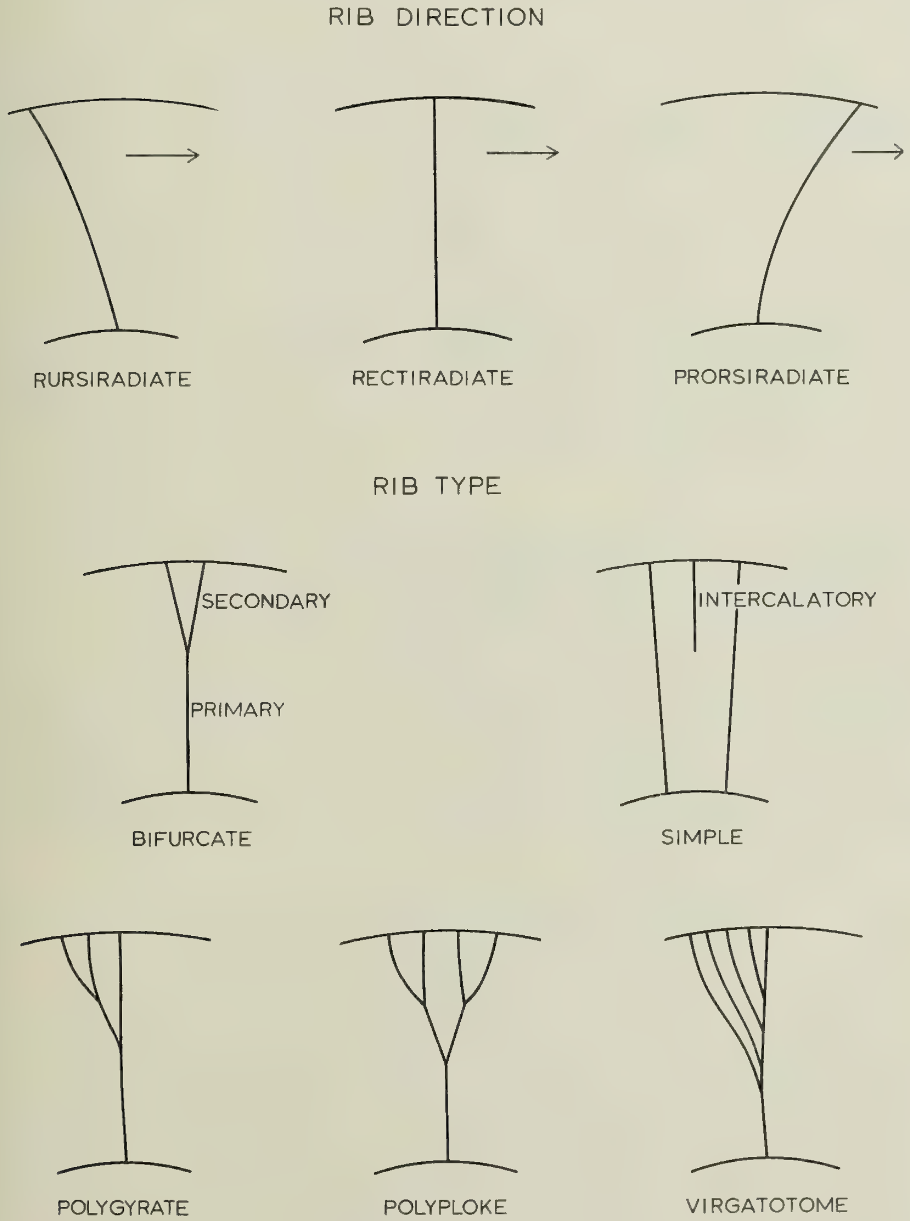

RIB DIRECTION
RURSIRADIATE
RECTIRADIATE
PRORSIRADIATE
RIB TYPE
SECONDARY
PRIMARY
BIFURCATE
INTERCALATORY
SIMPLE
POLYGYRATE
POLYPLOKE
VIRGATOTOME

FIG. 2. Rib directions and rib types occurring in the ammonites of the Upper Kimmeridge Clay.

original diameter was probably around 240 mm. There is a very close resemblance to the neotype (Hahn 1963, pl. 9, fig. 1), the only discernible difference being that the Dorset specimens still have quite prominent secondary ribs on the venter at the aperture.

REMARKS. This species is extremely rare in Dorset, two other specimens exist in the collections of Spath in the British Museum and are also from the same horizon. Salfeld recorded " numerous examples " of *G. gravesiana* from about this horizon (Arkell 1933 : 440). This species appears, however, to occur higher in the succession.

Gravesia cf. ***gravesiana*** (d'Orbigny)

(Pl. 1, fig. 2)

1850 *Ammonites gravesianus* d'Orbigny : 559, pl. 219, figs. 1, 2.

1963 *Gravesia gravesiana* (d'Orbigny) ; Hahn : 99, pl. 10, figs. 3, 4 ; pl. 12, figs. 3, 4 ; pl. 13, fig. 2. (See also for earlier references.)

MATERIAL. Two specimens.

STRATIGRAPHICAL RANGE. From 8 ft. below to 6 ft. above the Yellow Ledge Stone Band.

DESCRIPTION. Both the specimens are whorl fragments. The larger (Pl. 1, fig. 2) shows the ribbing very well and is very close to *G. gravesiana*. The total estimated crushed diameter of this specimen would be about 160 mm.

The other specimen shows only three primary ribs, with internal moulds of the secondary ribs, but is similar in rib style to the first specimen.

REMARKS. Salfeld recorded *Gravesia irius* at about this horizon, a species which the author was not able to find.

The occurrence of *Gravesia* above the Yellow Ledge Stone Band has not hitherto been reported, but as this genus is so rare in Dorset it is by no means certain that the newly established range of 60 feet in Dorset is the maximum range of this genus.

Subfamily **VIRGATOSPHINCTINAE** Spath 1923

Genus ***PECTINATITES*** Buckman 1922

Type species *Ammonites pectinatus* Phillips 1871.

DIAGNOSIS. Dimorphic. Microconchs generally 65–110 mm. in diameter, occasionally larger. Inner whorls with sharp biplicate ribbing, becoming a little coarser on body-chamber with occasional simple and trifurcate ribs. Peristome with ventral horn. Body-chamber generally half a whorl long. Macroconchs generally 140–200 mm. occasionally larger, very rarely smaller. Inner whorls with sharp biplicate ribbing. Outer whorl very variable, usually with strong primary ribs and two to five secondary ribs to each primary rib. Peristome simple. Body-chamber generally half a whorl long. Constrictions present in some species.

Upper Kimmeridgian. (Elegans to Pectinatus Zones).

Sexual Dimorphism

Detailed collecting from the Upper Kimmeridge Clay at the type-section at Kimmeridge, Dorset, has revealed many ammonites referable to species of the genus *Pectinatites* Buckman. Random sampling has established that the vast majority of these fall into one of two size groups. Formerly it has been considered by those who had collected ammonites from this section (e.g. Arkell & Spath), that the smaller specimens were merely young forms of the larger. However, these previous collections consist mostly of individuals from which the peristome had been broken during extraction from the rock, and examination of recent collections, consisting mainly of individuals with peristome intact, suggests a new interpretation of the size grouping. This interpretation arises from the fact that at every horizon from which collections were made, only two size groups are found. The smaller size falls into the 65–110 mm. diameter range, and the larger into the 140–200 mm. diameter range. If the ammonites of the smaller size group were the young of the larger ones it would be remarkable not to find, at some horizon, ammonites falling into the size range 110–140 mm. diameter. Evidence to show that the two groups are quite distinct follows below.

Callomon (1963 : 25) has summarized the criteria by which an ammonite may be judged to be mature. These are:

(a) Uncoiling of the umbilical seam.
(b) Modification of sculpture near the peristome; usually a coarsening and re- or degeneration of ribbing, but often with terminal constrictions, ventral collars, flares, horns, rostra, lateral lappets etc.
(c) Approximation and degeneration of the last few septal sutures.

As the ammonites are badly crushed, all traces of the septa have been destroyed. If, however, the first two of these criteria are applied, it is found that both size groups mentioned above consist of mature individuals.

Species of these perisphinctid ammonites are best distinguished from one another by the density of the ribbing. If the numbers of ribs at given diameters are plotted against diameters on a graph, a curve is produced which is distinctive for any given species. The two size groups under consideration here give generally similar, but not identical curves, so that it is possible to distinguish, by means of rib curves, the larger from the smaller type, even with incomplete material. These two groups have been referred to as microconchs and macroconchs by Callomon (1957 : 62), a terminology which has become generally accepted.

The microconchs, in this case, are generally small forms with a diameter of 65–110 mm., but at one horizon they range up to 185 mm. in size. In all cases the ribbing is of normal perisphinctid biplicate style and, apart from slight coarsening towards the aperture and occasional development of polygyrate ribs, shows little modification. The aperture bears a horn-like process projecting from the venter. The umbilical seam gradually uncoils over the last half whorl, so that at the aperture many forms are completely evolute. The apertural margin is sometimes devoid of ribbing and shows a smooth zone, ornamented little, save for growth lines, and the presence of the ventral horn.

The macroconchs are usually 140–200 mm. in diameter, but occasionally are larger, or very rarely smaller, and are characterized by a smooth sinuous peristome margin. The ribbing on the inner whorls is of a simple biplicate style, but the point of bifurcation usually occurs slightly higher on the whorl side than it does on the microconchs. The body-chamber develops irregular ribbing and, particularly in the forms from higher horizons, has a tendency to fasciculation or virgatotomy. Uncoiling of the umbilical seam occurs only over the last half whorl.

The two forms are found in association throughout the succession, although the ratio of microconchs to macroconchs varies. This ratio is usually within the limits 2 : 1–1 : 2. Where only a few specimens have been obtained from one horizon this ratio is not treated as significant.

That these two groups of ammonites are very closely related is strongly suggested by their co-existence at each fossiliferous horizon, their identical stratigraphical range, and their similar rib curves. However, four specimens from one horizon (13 feet above the Rope Lake Head Stone Band) from which have been collected 32 microconchs and 34 macroconchs, show conclusively the relationship. Three of these specimens appear to be normal macroconchs, but have on their inner whorls structures resembling those of the horn of the microconch. However, this structure differs from the true microconch horn; it has negligible ventral projection, it is developed from a single rib, and it projects laterally.

The fourth of these specimens is unique in that it is intermediate in size between the two groups (117 mm. diameter), has the typical microconch horn developed, but shows the beginnings of the macroconch type of ribbing associated with four further horns. The rib density of the first three of the ammonites shows them to have affinity with the macroconch group. The fourth specimen has a rib density intermediate between that of a microconch and a macroconch.

The undersides of the ammonites, as they lie in the rock, are quite often encrusted with oysters, although the upper surface is generally free of them. It would, therefore, seem that the oysters attached themselves to the ammonite conch after the death of the latter, otherwise the oysters would presumably be equally common on both surfaces. They apparently grew in the shelter provided by the umbilical space beneath the ammonite, and flourished there until continued sedimentation eventually killed them. Medcof (1955) has shown that modern oyster larvae prefer to settle on under-surfaces. In this case the ammonite shells would provide the only such surfaces available on the sea bed.

Judging by the size of these oysters, a considerable time must have elapsed before they were killed by the continued influx of sediment, so that we may reasonably conclude that sedimentation was not rapid. This is also supported by lithological evidence. The rocks are a fairly uniform argillaceous series—grey and black shales and clays with occasional cementstone bands—and, apart from lamination, are devoid of sedimentary structures.

Save for the very occasional juvenile forms and occasional gerontic forms, all the ammonites fall into one of the two size groups mentioned previously, and bearing in mind the evidence of slow deposition, it is likely that the ammonite faunas of the Upper Kimmeridge Clay in Dorset represent a death assemblage.

Taking into account the evidence of maturity of the ammonites, and the fact that they represent death assemblages, it would appear evident that the difference in size of the two groups is of a fundamental nature. It seems most unlikely that current sorting of the shells, or sudden extermination of whole populations occurred. The most obvious interpretation of this size distribution is that these ammonites exhibit dimorphism. Dimorphism of ammonite shells is probably an expression of some difference which was present in the soft parts also. The most obvious difference between dimorphs would appear to be a sexual one, and there is some evidence to suggest that the microconch and macroconch may represent the two sexes.

Examination of the microconchs yields several important facts relating to the horn. It is never developed until a diameter of at least 60 mm. (generally more) is attained. In other words, the horn is not developed until a certain stage of growth is reached. At various growth stages beyond this diameter further horns may be developed, but the presence of a former horn or horns is always detectable. Sometimes the earlier horn is retained, and in other cases the earlier horns appear to have been shed, and to have left behind a characteristic scar on the venter.

Apart from the four macroconch specimens mentioned earlier, none shows any trace on the earlier whorls of any type of horn or ventral scar.

In section, the microconch horn is U-shaped, opening forwards. This suggests that it housed some part of the soft parts of the animal, and, since the horn is confined to the microconch, it is reasonable to assume that its function may have been sexual. This would explain its confinement to the microconch, and its occurrence only in nearly full-grown specimens.

The four specimens showing characteristics of each group can then be explained as various degrees of intersexual specimens. Three of them are barely distinguishable from true macroconchs, but the fourth appears to be a true intersex.

As mentioned above, the macroconchs and microconchs differ somewhat in the density of their ribbing. At 15 mm. diameter (the smallest diameter at which it is practicable to count the ribs accurately) the macroconchs are nearly always finer ribbed than the corresponding microconchs. The comparative density of the ribbing of the two forms, at greater diameters, is seen to vary with the species concerned. Presumably, both microconch and macroconch reached maturity at the same age, so that the rate of growth of the macroconch must have been greater than that of the microconch. This would appear to explain these discrepancies, since growth rate in each species must, to perhaps a small and varying extent, have had an effect on the density of the ribbing.

Our knowledge of the soft parts of ammonites is almost entirely based on analogy with modern cephalopods, particularly *Nautilus*. In most living cephalopods the male of the species is smaller than the female. In *Nautilus*, however, the male is slightly broader-shelled than the female, the extra breadth of the shell being utilised to incorporate the male copulatory organs, the diameter of the two shells is approximately equal. It appears, therefore, that in any case of marked dimorphism in modern cephalopods the male is the smaller sex, and it therefore appears likely that in *Pectinatites* the microconch represents the male of the species. If this were so, the horn may have assisted in copulation. If the spadix (the copulatory organ of the male cephalopods) were housed within the horn, by insertion of the horn within the venter of the female shell, fertilization of the ova would be more readily assured.

Dimorphism has been reported in other groups of ammonites by various authors (e.g. Callomon 1963, Makowski 1962, Westermann 1964). In many of the reported instances, the microconch aperture bears a pair of lappets developed laterally. Lappets are not present in any ammonites found hitherto from the Upper Kimmeridge Clay, while the horn of the Kimmeridgian microconchs is apparently unique to this group of ammonites. These horned Kimmeridgian forms are known outside Britain from Northern France and Greenland, and, as they appear to have evolved rapidly, promise much in precise correlations within this Upper Jurassic faunal province.

Interpretation of PECTINATITES

The genus *Pectinatites* was originally proposed for a few closely related species from the Pectinatus Zone of Oxfordshire. The Pectinatus Zone there is to be correlated with the rocks between the White Stone Band, and the base of the *Pavlovia rotunda* Zone in the Dorset succession.

As early as 1896 Hudleston (1896 : 322) had remarked on the similarity between *Ammonites pectinatus* and the pyritized ammonites which occur at the top of the Kimmeridge Oil Shale or Blackstone, about 150 ft. below the White Stone Band in the Kimmeridge section.

Buckman, in June 1925, assigned one species of these pyritized ammonites from the Blackstone to a new genus, *Pectiniformites* which he placed six hemerae earlier than his *Pectinatus* hemera, but Neaverson (Dec. 1925) did not accept Buckman's findings, and placed these Blackstone ammonites in the genus *Pectinatites*. Spath (1936 : 18) in turn placed them in his genus *Subplanites* proposed in 1925.

Herein, I place these ammonites in the genus *Pectinatites*, in which I recognize three subgenera: *Pectinatites* (sensu stricto); *Virgatosphinctoides;* and *Arkellites* subgen. nov.

Many generic attributions have been given to species of *Pectinatites* in the past. These generic names, for the most part, belong to quite distinct genera many of which do not occur in Britain, while others of them are either junior synonyms, or in some cases subgenera of *Pectinatites*. As much confusion, and many unreliable correlations have been made on the basis of misidentification of species of *Pectinatites* with other genera, there follows a discussion of these genera and their relationship, if any, to *Pectinatites*.

VIRGATITES Pavlow 1892

TYPE SPECIES. *Ammonites virgatus* von Buch 1832. (Subsequently designated Douvillé 1910.)

This genus was recorded from the horizon of the Kimmeridge oil-shale by Salfeld (1913), and a zone of *V. miatschkovensis* introduced by him for the beds between the *Gravesia* zones and his zone of *Perisphinctes pallasianus* (= modern Pectinatus Zone). The genus is characterized by virgatotome ribbing on the inner whorls, sometimes reverting to simple or bifurcate ribbing on the body-chamber. All the Dorset ammonites from this part of the Kimmeridge Clay have normal perisphinctid bifurcate ribs on their inner whorls, and it is only on the outer whorl that virgatotome ribbing may develop. There is now no doubt that *Virgatites* is much younger in age than these Kimmeridge forms, and appears to be restricted to the Volgian faunal province of eastern Europe.

PSEUDOVIRGATITES Vetters 1905

TYPE SPECIES. *Ammonites scruposus* Oppel *in* Zittel 1868.

Lamplugh, Kitchin & Pringle (1923 : 222) recorded the occurrence of the genus *Pseudovirgatites* from Dorset, and introduced a zone of *Pseudovirgatites* to include the horizon of the Blackstone in Dorset. This genus is often homeomorphic with the genus *Pectinatites*. The type species from the Lower Tithonian has similar rib-style on its outer whorl to that of some large species of *Pectinatites* (e.g. *P*. (*Virgatosphinctoides*) *pseudoscruposus* (Spath)). Other species of *Pseudovirgatites*, such as some of those recently figured by Donze & Enay (1961) and Michailov (1964), are remarkably homeomorphic with some species of *Pectinatites* (e.g. *P*. (*P*.) *inconsuetus* sp. nov. See p. 138, Pl. 30). The microconch of *Pseudovirgatites* does not, however, possess a ventral peristomal horn as does *Pectinatites*, and all records of *Pseudovirgatites* from Britain would appear to refer to homeomorphic forms of *Pectinatites*.

LITHACOCERAS Hyatt 1900

TYPE SPECIES. *Ammonites ulmensis* Oppel 1863.

The inner whorls of *Lithacoceras* generally bear fine bifurcate ribs which modify on the outer whorl of the macroconch to produce in the type-species widely-spaced blunt primary ribs, each giving rise to up to eight secondaries. Some species of the genus reach a very large size. There is often a considerable degree of homeomorphy between species of this genus and species of *Pectinatites*. Apart from peristomal differences, the microconchs of the two genera can be very similar, and the middle whorls of a macroconch of *Lithacoceras* sometimes very closely approach the ornament of the macroconch of *Pectinatites*. This homeomorphy has misled many workers in the past. In particular the species of *Pectinatites* from the Hen Cliff Shales have been identified in the past as *Lithacoceras*. (e.g. Arkell 1956 : 21).

PECTINATITES Buckman 1922

TYPE SPECIES. *Ammonites pectinatus* Phillips 1871.

The name *Pectinatites* is the most senior available name for the British Upper Kimmeridgian ammonites described herein. It is distinguished from all other genera which are to varying degrees homeomorphic with it, by its type of dimorphism. As these ammonites with horned microconchs form a closely related natural group, it is here proposed to include all such dimorphic forms in this genus.

WHEATLEYITES Buckman 1923

TYPE SPECIES. *Wheatleyites tricostulatus* Buckman 1923.

This genus is characterized by finely-ribbed inner whorls, which modify to produce an outer whorl with coarse widely-spaced primary ribs; the secondary ribs gradually fade on the body-chamber. Some forms of *Wheatleyites* are homeomorphic with species of the Tithonian genus *Pseudovirgatites*. *Wheatleyites* is here regarded as a junior synonym of *Pectinatites*, it being a name applied by Buckman to macroconchs of *Pectinatites* having this particular type of modification of the ribs on the outer whorls.

SUBPLANITES Spath 1925 (January)

TYPES SPECIES. *Virgatosphinctes reisi* Schneid 1914.

To this genus belong a complex of forms occurring in the Tithonian rocks of Europe. Characteristically their inner whorls bear fine bifurcate ribs, which are modified on the body-chamber in a fashion similar to that which obtains in many species of *Pectinatites*. It was for this reason that many of the British species of *Pectinatites* were long considered to be species of *Subplanites*. *Virgatosphinctoides* Neaverson (here treated as a subgenus of *Pectinatites*), was considered a junior synonym of *Subplanites*. This undetected homeomorphy led to the establishment of a number of unreliable correlations between Britain and Southern Europe.

The microconchs of *Subplanites* bear lappets, and are for this reason easily distinguishable from the microconchs of *Pectinatites* when material with intact peristomes is available, but in the absence of specimens with peristomes it is virtually impossible to distinguish the two genera.

All the British forms appear to belong to *Pectinatites*, but in the case of such faunas as those from Russia, recently described by Michailov (1964), it is not possible to determine the genus of ammonites present owing to the incomplete nature of the material.

PECTINIFORMITES Buckman 1925 (June)

TYPE SPECIES (by monotypy). *Pectiniformites bivius* Buckman 1925.

The holotype which is in the Dorset County Museum, Dorchester, is a pyritic cast from the Blackstone. The pyrite of the outer whorl has in places reached an advanced state of decomposition, and the specimen is now of little value. There is also in this museum, however, a cast of the holotype made in 1925, which appears to correspond very closely in dimensions to the holotype, and which is a better specimen than the holotype in its present condition.

Buckman marked on his plate of the holotype (1925, pl. 568) the position of the last visible suture, which is just one whorl back from the supposed peristome. However, the type of preservation in the Blackstone (solid pyrite) generally destroys all trace of the septa, and in the author's opinion, the septum marked by Buckman was the last *visible*, but not the last occurring septum. This view is supported by the occurrence of better-preserved ammonites having affinities with this species and with a short body-chamber. (E.g. *Pectinatites pectinatus* (Phillips) Buckman 1922, pl. 354B, which shows five-eighths of a whorl of body-chamber; and the length of the body-chamber estimated from differences in the degree of crushing of the Dorset material, which suggests a body-chamber length of between three and five-eighths of a whorl. No specimen of *Pectinatites* is known to the author with a body-chamber as much as one whorl in length).

The ammonites from the Blackstone are largely uncrushed, but there is another, more important, difference between the ammonites from this horizon and other horizons in the Dorset succession. In the Blackstone, ammonites of all growth stages are preserved, from very small nuclei to specimens over 150 mm. in diameter. This contrasts with other horizons where mature individuals make up by far the greater part of the ammonite fauna. Furthermore, no ammonites have been collected (or preserved?) in the Blackstone with intact peristomes. This means that it is not possible, in the case of the smaller specimens, to distinguish macroconchs from microconchs, and thus that the interpretation of *Pectininformites* is open to doubt.

Further, the Blackstone has hitherto failed to yield macroconchs with well-preserved inner worls, so that the holotype of *Pectiniformites bivius* cannot be compared to any known macroconch specimen. It is, therefore, not possible to determine to which subgenus of *Pectinatites* this species belongs. The rib density is such that affinity with *Arkellites* subgen. nov. is unlikely (approximately 55 ribs at 30 mm. diameter). It may possibly therefore be consubgeneric with *Virgatosphinctoides*, but there appears to be no over-riding reason why it should not equally be placed in *Pectinatites, sensu stricto*. This was also the view of Neaverson (1925 : 15) " Buckman has recently instituted a new genus *Pectiniformites* for ammonites of the *pectinatus*-type from this facies (the oil shales of Kimmeridge). There seems to be no justification for this, and *Pectiniformites* must be regarded as synonymous with *Pectinatites* ".

Pectiniformites would thus become a junior synonym of *Pectinatites*, and is so treated here.

KERATINITES Buckman 1925 (October)

TYPE SPECIES. *Keratinites keratophorus* Buckman 1925.

This genus was introduced by Buckman for ammonites from the Pectinatus Zone having a peristome bearing a ventral horn. These forms are the microconchs of *Pectinatites*, and the name *Keratinites* is here regarded as a junior synonym of *Pectinatites*.

VIRGATOSPHINCTOIDES Neaverson 1925 (December) : 11

TYPE SPECIES. *Virgatosphinctoides wheatleyensis* Neaverson 1925.

This genus is characterized by finely ribbed inner whorls which are modified on the body-chamber of the macroconch, often producing polygyrate, polyploke, or virgatotome ribbing. The genus was regarded by Spath as synonymous with, or at the most subgenerically different from, his genus *Subplanites* proposed a few months earlier (see above). Systematic collections from Dorset have now established that

Virgatosphinctoides is dimorphic. The microconchs bear a ventral horn and are never seen to have lappets. *Virgatosphinctoides* is thus easily distinguished from *Subplanites* when material with intact peristomes is available. The presence of a horned peristome, however, shows that *Virgatosphinctoides* is closely related to *Pectinatites*. The microconchs of the two are sometimes indistinguishable, and only the characters of the macroconchs can usefully separate the two forms. For this reason *Virgatosphinctoides* is here treated as a subgenus of *Pectinatites*.

ALLOVIRGATITES Neaverson 1925 (December) : 29

Type species. *Allovirgatites woodwardi* Neaverson 1925.

Neaverson's basis for distinction between *Virgatosphinctoides* and *Allovirgatites* appears to have been based almost entirely on differences in the septal suture of species of the two genera. However, the rib-style and its development is very similar in these two forms, and there appears to be little justification for drawing distinction between them. Neaverson admitted similarity between the suture lines of these two genera in the young stages, and there would seem little doubt that differences between his described forms are no more than specific differences. *Allovirgatites* is therefore here regarded as a junior synonym of *Virgatosphinctoides*.

SUBDICHOTOMOCERAS Spath 1925 (January)

Type species. *Subdichotomoceras lamplughi* Spath 1925.

This genus is characterized by sharply biplicate ribbing throughout development, together with deep constrictions which are bordered by simple ribs. The aperture is without lappets. The holotype came from the Eudoxus Zone of Yorkshire, and the genus does not appear to be represented in higher Kimmeridgian deposits in Dorset.

SPHINCTOCERAS Neaverson 1925 (December)

Type species. *Sphinctoceras crassum* Neaverson 1925.

Two species of *Sphinctoceras* were described by Neaverson from the Wheatleyensis Zone of Oxfordshire. They are massive inflated forms with coarse strong biplicate ribs. There seems little doubt that *Sphinctoceras* is closely related to *Subdichotomoceras*, the former being almost certainly the macroconch of the latter. No specimens of *Sphinctoceras* have hitherto been found in Dorset, but the genus is mentioned here because the conservative " biplex " stock to which it belongs gave rise to the pavlovids in the Pectinatus Zone. The sharp biplicate ribbing, the very high point of bifurcation of the ribs, and the absence of polygyrate ribs and any marked apertural modification make identification of these forms with more coarsely-ribbed species of *Pectinatites* unlikely.

The origins of PECTINATITES

The origins of *Pectinatites* are rather obscure, but there is one feature of the ribbing which must be considered of great value in deducing the origin of the genus. This is the presence of the polygyrate, and more rarely the polyploke rib type (Geyer 1961, text-fig. 1). This type of ribbing, which is first found in some Upper Oxfordian ammonites, is the first new character in perisphinctid ornamentation to appear since the Bajocian, and it therefore appears very probable that all ammonites which have this rib style are related.

In the Lower Kimmeridgian genus *Ataxioceras*, the development of polygyrate ribbing reaches its extreme. *Ataxioceras* is also often ribbed in a most irregular fashion, a character which is evident in many species of *Pectinatites*. A further character of *Ataxioceras* is of importance too in tracing the origin of *Pectinatites*. This is the apertural modification of the microconch. Most microconchs of *Ataxioceras* appear to have well-developed lappets (e.g. Geyer 1961*a*, pl. 14, fig. 2), but there are specimens which appear to have a horn developed (e.g. Geyer 1961*a*, pl. 13, fig. 5). It thus appears that three of the most important characters of *Pectinatites* are also found in *Ataxioceras*.

There must also be taken into account the remarkable similarity of some species of *Pectinatites* to species of the Tithonian genera *Subplanites*, *Lithacoceras*, and *Pseudovirgatites*. There can be no doubt that there was a marine connection between Britain and the Swabia–Franconia area at least for a short while after the Lower Kimmeridgian, since the genus *Gravesia* is common to both areas. However, there are apparently no substantiated records of *Lithacoceras* or *Subplanites* from the Lower Kimmeridgian of Britain. (In this respect I cannot accept Arkell's report of *Lithacoceras* from the *Aulacostephanus* zones (1947 : 73); or that of Ziegler of *Subplanites rueppellianus* from the same beds (1962 : 13)). All reported instances of these genera must, in the absence of any figured evidence to the contrary, be interpreted as occurrences of hitherto undescribed perisphinctids which in the author's opinion do not belong either to *Subplanites* or *Lithacoceras*.

The difference between *Subplanites* and *Lithacoceras* on the one hand, and *Pectinatites sensu lato* on the other hand has not been recognized hitherto owing to the failure to take note of the different types of dimorphism in the two faunal provinces. As shown above, the microconchs of *Pectinatites* are horned, the macroconchs have a straight peristome and often a tendency towards virgatotome ribbing on the body-chamber.

Subplanites and *Lithacoceras* both have lappeted microconchs, so that microconchs with intact peristomes are easily distinguishable from microconchs of *Pectinatites*. However, several species of microconchs of *Subplanites* such as *S. reisi*, *S. schlosseri*, and *S. moernsheimensis* have polygyrate ribbing on their body-chamber, and are similar in adult size and rib-style to macroconchs of species of *Pectinatites*, but differ in that the former bear lappets whereas the latter do not. When material without intact peristomes is compared, therefore, the two forms are virtually indistinguishable. Similarly *Lithacoceras* can be confused with *Pectinatites* when peristomes are not intact. Thus, previous comparisons of the British Kimmeridgian fauna to the Tithonian fauna have been comparisons between Kimmeridgian macroconchs and Tithonian microconchs. The similarity of the two faunas therefore must be regarded as an example of penecontemporaneous homeomorphy.

However the similarity of the rib-style of the two faunas, in particular the presence of polygyrate ribbing, strongly suggests that they were derived from the same stock. This presumably lay in some of the less specialized of the Lower Kimmeridgian ataxioceratids, or in such a genus as the Upper Oxfordian *Discosphinctes* which has some polygyrate ribs on the body-chamber.

This being the case it would seem that *Lithacoceras* should be classified together with *Subplanites* and *Pectinatites* in the same sub-family. Arkell (1957) placed *Lithacoceras* in the sub-family Ataxioceratinae (Buckman 1921) whilst *Subplanites* and *Pectinatites* were assigned by him to the sub-family Virgatosphinctinae (Spath 1923). Since these three genera are presumed to be derivatives of the ataxioceratid stock, and not themselves ataxioceratids, they perhaps should be all placed together in the sub-family Virgatosphinctinae.

Subgenus ***ARKELLITES*** nov.

TYPE SPECIES. *Pectinatites* (*Arkellites*) *hudlestoni* sp. nov.

DIAGNOSIS. Dimorphic. Microconchs fairly coarsely ribbed on inner whorls. Body-chamber generally more coarsely ribbed than inner whorls. Horn sometimes little more than an inflation of ventral part of peristome. Macroconchs with similarly ribbed inner whorls to those of microconchs. Outer whorl showing little or no variocostation, ribs little changed to the peristome. Some species showing strengthening of primary ribs with development of intercalatory secondary and unbranched primary ribs. Polygyrate ribs generally rare. Peristome simple. Constrictions if present shallow. Suture line unknown.

Upper Kimmeridgian, Elegans to Hudlestoni Zones, ? Lower Pectinatus Zone.

Pectinatites **(*Arkellites*)** ***primitivus*** sp. nov.

(Pl. 2, figs. 1, 2; Pl. 3)

DIAGNOSIS. Macroconchs 125–150 mm. in diameter, with following rib densities: at 15 mm. 30–32 ribs; at 20, 32–34; 25, 33–35; 30, 33–36; 35, 36–37; 40, 37–38; 45, 37–38; 50, 39; 55, 40; 60, 41; 65, 43. Ribs rectiradiate to prorsiradiate with wide angle of furcation. Outer whorl variable but typically with frequent unbranched primary ribs. Microconchs 80–105 mm. in diameter, with following rib densities: at 15 mm. 32 ribs; at 20, 32–36; 25, 33–37; 30, 34–38; 35, 35–38; 40, 36–40. Ribs rectiradiate or slightly prorsiradiate. Outer whorl variable with bifurcate ribs predominating, sometimes with polygyrate and simple ribs, and intercalatory secondaries. Peristome slightly inflated ventrally.

HOLOTYPE. Macroconch C.73392.

PARATYPE. Macroconch C.73393.

PARATYPES (ALLOTYPES). Microconchs C.73394, C.73395.

MATERIAL. Nine specimens (four macroconchs, five microconchs).

HORIZON. Holotype, paratype and allotype C.73394, from 25 ft. below the Yellow Ledge Stone Band. Allotype C.73395 from 55 ft. below this band.

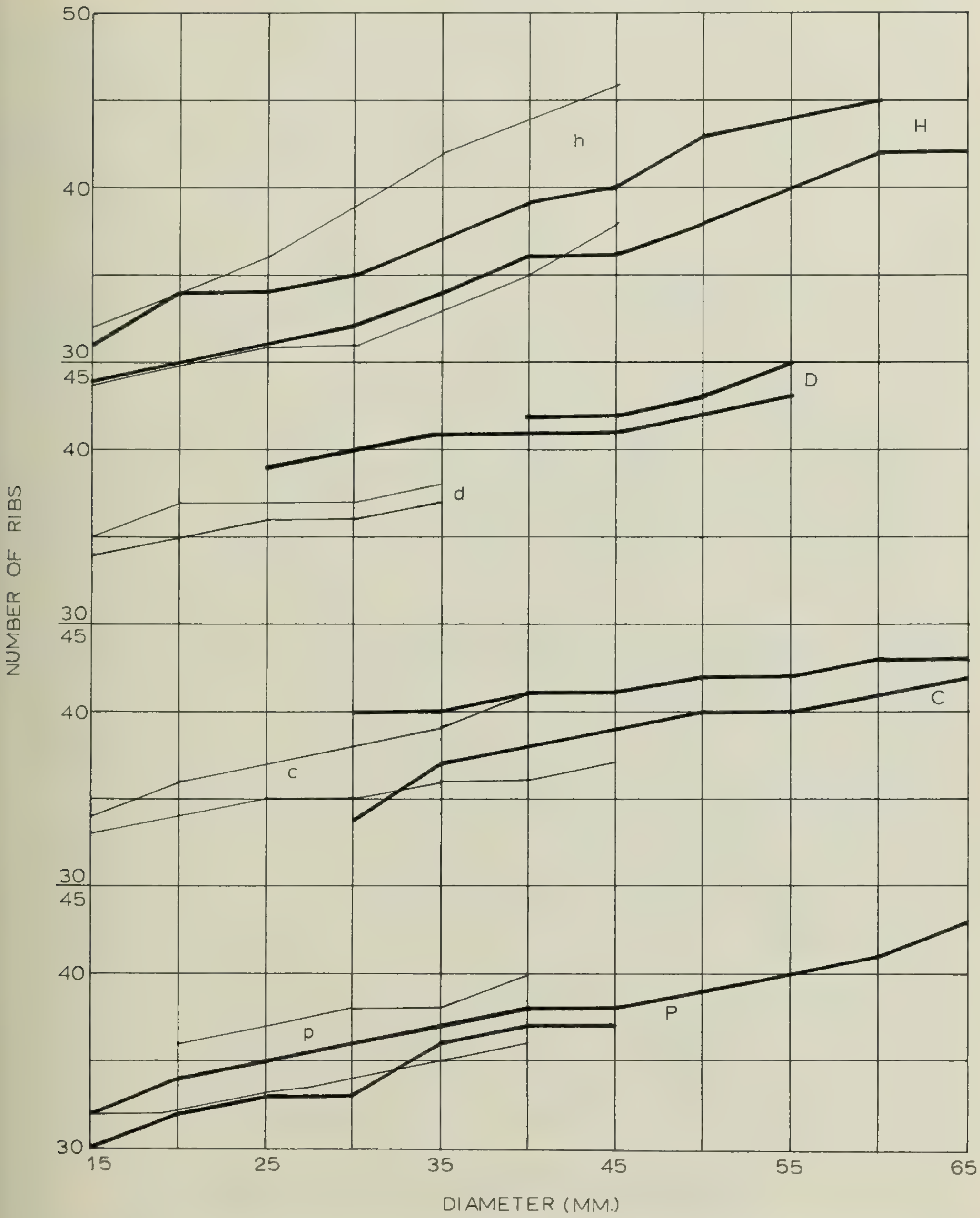


FIG. 3. Rib density of species of the subgenus *Arkellites*. Upper case letters : macroconchs ; lower case letters : microconchs. H, h : *P.* (*A.*) *hudlestoni* ; D, d : *P.* (*A.*) *damoni* ; C, c : *P.* (*A.*) *cuddlensis* ; P, p : *P.* (*A.*) *primitivus*.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Elegans Zone, between 12 and 55 ft. below the Yellow Ledge Stone Band (see below).

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 125–150 mm. Diameter of umbilicus 49–65 mm. The last whorl of the holotype has 54 primary and 76 secondary ribs, while the last whorl of the paratype has approximately 48 primary and 90 secondary ribs. At 20 mm. diameter there are 34 ribs; at 25, 35; 30, 36; 35, 36; 40, 37; 45, 37–38; 50, 39; 55, 40; 60, 41; 65, 43. The paratype has a similar rib-density.

The ribs on the inner whorls are rectiradiate at the umbilical shoulder, then sweep forward to become prorsiradiate. (The few apparently rursiradial ribs on the holotype have been distorted by crushing.) The point of bifurcation of the ribs is high on the whorl side. The umbilical seam gradually uncoils over the last half-whorl. The ribs on the outer whorl are either bifurcate or simple. The angle of bifurcation is larger than in most of the species of this subgenus. The holotype shows no fewer than 19 simple ribs on its outer whorl. The paratype has fewer simple ribs (approximately 9) and at least one trifurcate rib.

Microconch. Evolute shell with a diameter of between 80 and 105 mm. Diameter of umbilicus 32–40 mm. The last whorl of paratype C.73395 has approximately 45 primary and 103 secondary ribs. At 15 mm. diameter there are 32 ribs, at 20, 32–36; 25, 33–37; 30, 34–38; 35, 35–38; 40, 36–40.

The ribs on the inner whorl are rectiradiate at the umbilical shoulder but curve forwards and become straight and slightly prorsiradiate for the rest of their length. The point of bifurcation of the ribs is high on the whorl side. The umbilical seam uncoils over the last half whorl. The ribs on the outer whorl gradually become straight and rectiradiate. There are three simple ribs on the last whorl of paratype C.73394, otherwise the ribs are bifurcate. The other paratype shows several polygyrate ribs on the last whorl. The peristome is slightly inflated ventrally.

REMARKS. The macroconch of this species shows features which are interpreted as being primitive characters of the genus. These include the wide angle of furcation of the ribs, the abundant unbranched primary ribs, and the relative absence of trifurcate (polygyrate) ribs. The microconchs exhibit only a feeble ventral inflation of the peristome. The outer whorl of allotype C.73395 shows resemblance in its rib-style to microconchs of species of the sub-genus *Virgatosphinctoides*, but the coarser ribbing of the inner whorls of the former provides easy distinction. It is possible, however, that the subgenus *Virgatosphinctoides* was derived from this species.

Incomplete and poorly preserved ammonites from the lowest Hen Cliff Shales, and their basal cementstone, may belong to this species. This would extend the range of the species down to 70 feet below the Yellow Ledge Stone Band.

Pectinatites* (*Arkellites*) *cuddlensis sp. nov.

(Pl. 4; Pl. 5, fig. 1)

DIAGNOSIS. Large stoutly-ribbed *Arkellites*. Macroconchs 160–210 mm. in diameter, with following rib densities: at 30 mm., 34–40 ribs; at 35, 37–40; 40, 38–41;

45, 39–41; 50, 40–42; 55, 40–42; 60, 41–43; 65, 42–43. Ribs rectiradiate to slightly prorsiradiate. Outer whorl with mainly bifurcate ribs, but some unbranched primary and occasional polygyrate ribs, and intercalatory secondary ribs. Microconchs 110–128 mm. in diameter, with following rib densities: at 15 mm., 33–34 ribs; at 20, 34–36; 25, 35–37; 30, 35–38; 35, 36–39; 40, 36–41; 45, 37. Ribs of inner whorls similar in style to macroconch. Peristome with ventral horn 6–21 mm. long.

HOLOTYPE. Macroconch C.73396.

PARATYPE (ALLOTYPE). Microconch C.73397.

MATERIAL. Nine specimens (five macroconchs, four microconchs).

HORIZON. Holotype from 18 ft. and paratype from 25 ft. above the Yellow Ledge Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, topmost Elegans to lower Scitulus Zones, 12 ft. below to 27 ft. above the Yellow Ledge Stone Band.

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 160–210 mm. The holotype has a diameter of 206 mm., and an umbilical diameter of 94 mm. There are 49 primary and 107 secondary ribs on the outer whorl of the holotype. At 30 mm. diameter the holotype has 34 ribs; at 35, 36; 40, 38; 45, 39; 50, 40; 55, 40; 60, 41; 65, 42; 70, 43; 75, 44; 80, 46; 85, 47; 90, 48. The variation in rib density within the species is shown in Text-fig. 3.

The ribs on the inner whorls are rursiradiate at the umbilical shoulder; they then swing forwards and become rectiradiate or slightly prorsiradiate and fairly straight. Some of the ribs on the inner whorls of the holotype are partially distorted by the crushing. The point of bifurcation of the ribs is high on the whorl-side. There is a slight uncoiling of the umbilical seam over the last half whorl.

The ribs on the outer whorl become stronger and their furcation somewhat irregular, with the development of intercalatory secondary ribs, unbranched primary ribs, occasional trifurcate ribs, and occasional furcation low in the whorl-side.

There do not appear to be any constrictions on the last whorl, although the rib style at one point (a trifurcate rib followed very closely by a simple rib) is very similar to that which obtains when a constriction is present.

The peristome is simple.

Microconch. Evolute shell with a diameter of 110–128 mm. Diameter of umbilicus 42–47 mm. The last whorl of the paratype has 43 primary and 89 secondary ribs. At 15 mm. diameter the paratype has 33 ribs; at 30, 34; 25, 36; 30, 38; 35, 39; 40, 41. The other microconchs of this species are similar to the paratype in rib density. (Text-fig. 3).

The ribs on the inner whorls are similar in style to those of the macroconch. The umbilical seam uncoils over the last half whorl, which appears to correspond to the length of the body-chamber. The ribs on the outer whorl coarsen slightly and are more or less straight and rectiradiate. There are occasional simple and trifurcate ribs on the last whorl.

The aperture bears a horn which is 21 mm. long on the paratype; the other complete microconchs have shorter horns.

REMARKS. This species has a similar, though not identical, density of ribbing on the inner whorls to that of *P.* (*A.*) *primitivus*, described above (p. 24). It differs, however, in adult size of both macroconch and microconch, and the density and style of ribbing of the outer whorl. It is probably, nevertheless, a derivative of this former species.

Pectinatites* (*Arkellites*) *damoni sp. nov.

(Pl. 5, figs. 2, 3; Pl. 6)

DIAGNOSIS. Macroconchs 136–160 mm. in diameter with following rib densities: at 25 mm. 39 ribs; at 30, 40; 35, 40–41; 40, 41–42; 45, 41–42; 50, 42–43; 55, 43–45. Ribs rectiradiate to slightly prorsiradiate. Outer whorl with irregular ribs with fairly wide angle of furcation, occasional unbranched primary ribs. No trifurcate ribs. Microconchs 70–90 mm. in diameter with following rib densities: at 15 mm. 34–35 ribs; at 20, 35–37; 25, 36–37; 30, 36–37; 35, 37–38. Ribs generally prorsiradiate. Outer whorl with occasional unbranched primary and polygyrate ribs. Peristome with ventral ribbed horn 3–15 mm. long.

HOLOTYPE. Macroconch C.73398.

PARATYPE. Macroconch C.73399.

PARATYPES (ALLOTYPES). Microconchs C.73400, C.73401.

MATERIAL. Sixteen specimens (four macroconchs, twelve microconchs).

HORIZON. Holotype and allotypes from 25 ft., paratype from 27 ft. above the Yellow Ledge Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, lower Scitulus Zone, ranging between 15 and 32 ft. above the Yellow Ledge Stone Band.

DESCRIPTION. *Macroconch.* Moderately evolute shell with a diameter of 130–160 mm. Diameter of umbilicus 54–60 mm. The holotype has approximately 41 primary ribs on the last whorl. No macroconch of this species with a complete last whorl has been found. At 25 mm. diameter the holotype has 39 ribs; at 30, 40; 35, 40; 40, 41; 45, 41; 50, 42; 55, 43; 60, 43. The variation in rib density within the species is shown in Text-fig. 3.

On the inner whorls the ribs are rursiradiate at the umbilical shoulder, they then swing forwards to become rectiradiate or slightly prorsiradiate and more or less straight. The point of bifurcation of the ribs is high on the whorl-side, and is not always visible on the innermost whorls. There is a slight uncoiling of the umbilical seam over the last half to three-quarters of a whorl.

The ribs on the outer whorl are rather " untidy " in appearance. They become coarser and have quite a wide angle of furcation. Occasional simple ribs are developed, but there is an absence of trifurcate ribs. No constrictions are visible.

Although no specimen has its peristome preserved intact, it is presumably simple.

Microconch. Evolute shell having a diameter of 70–90 mm. Diameter of umbilicus 25–35 mm. The last whorl of paratype C.73400 has 42 primary and 86 secondary ribs. The density of the ribs on the inner whorls can only be approximately determined on this specimen. Paratype C.73401 has 35 ribs at both 25 and 30 mm. diameter. Other microconchs of the species show similar rib densities (Text-fig. 3).

The ribs of the inner whorls are similar in style to those of the macroconch, but tend to be more prorsiradiate. On the outer whorl the forward inclination is not so pronounced, and the ribs approach the rectiradiate condition. The point of bifurcation of the ribs is quite high on the whorl-side, and is not always visible on the inner whorls. The umbilical seam uncoils gradually over the last half whorl. The length of the body-chamber (estimated by differences in the degree of crushing) is usually half a whorl long, but in some specimens it appears to be only about three-eighths of a whorl in length.

The ribs on the outer whorl are slightly coarser than those of the inner whorls. There may be several simple and occasional trifurcate ribs on the last whorl. The ventral part of the peristome bears a horn which varies in length from 3–15 mm. and is always quite strongly ribbed.

Remarks. The macroconch of this species shows some similarity with that of *P.* (*A.*) *primitivus*, described above (p. 24). It differs in the density of ribbing of the inner whorls. The respective microconchs are not likely to be confused on account of size, rib style and density, and horn development. This species may, however, be derived from *P.* (*A.*) *primitivus*. Adult size of both macroconch and microconch, and the very irregular ribbing of the outer whorl distinguished *P.* (*A.*) *damoni* from *P.* (*A.*) *cuddlensis*.

Pectinatites* (*Arkellites*) *hudlestoni sp. nov.

(Pl. 2, fig. 3; Pl. 7; Pl. 8, fig. 2)

Diagnosis. Large *Arkellites* with stout blunt ribs. Macroconchs 170–196 mm. in diameter with following rib densities: at 15 mm. there are 29–31 ribs; at 20, 30–34; 25, 31–34; 30, 32–35; 35, 34–37; 40, 36–39; 45, 36–40; 50, 38–43; 55, 40–44; 60, 42–45. Ribs rectiradiate to slightly rursiradiate. Ribs on outer whorl becoming blunt and massive, with abundant intercalatory secondary ribs and occasional unbranched primary ribs. Microconchs 72–112 mm. in diameter, with following rib densities: at 15 mm., 29–32 ribs; at 20, 30–34; 25, 31–36; 30, 31–39; 35, 33–42; 40, 35–44; 45, 38–46. Ribs approximately rectiradiate, branching fairly low on whorl-side. Ribs coarser on outer whorl with occasional simple and rare polygyrate ribs. Peristome with well-developed ventral horn 4–21 mm. long. Horn ornamented only by growth lines.

Holotype. Macroconch C.73403.

Paratype (allotype). Microconch C.73404.

Material. Twenty-four specimens, including eleven plaster casts. Five macroconchs, nineteen microconchs.

Horizon. Holotype and paratype from shales 13 ft. above the Rope Lake Head Stone Band.

Stratigraphical range. Upper Kimmeridgian, Hudlestoni Zone, from 12 ft. above the Rope Lake Head Stone Band to 9 ft. below the White Stone Band.

Description. *Macroconch.* The dimensions given below are from the holotype which is the only reasonably complete macroconch which is well-preserved.

Stoutly ribbed evolute shell with a diameter of 196 mm. Diameter of the umbilicus 93 mm. There are 42 primary and 96 secondary ribs on the last whorl. At 15 mm. diameter there are 31 ribs; at 20, 32; 25, 32; 30, 33; 35, 34; 40, 36; 45, 36; 50, 38; 55, 40; 60, 42; 65, 42; 70, 43; 75, 44; 80, 45; 85, 46; 90, 46. The variation in rib density is shown in Text-fig. 3.

The ribs on the inner whorls have a slight rursiradial curve at the umbilical shoulder; for the rest of their length they are straight and rectiradiate, or slightly rursiradiate. The point of bifurcation is high on the whorl-side apart from occasional ribs which branch near the umbilical shoulder. The umbilical seam uncoils over the last five-eighths of a whorl.

On the outer whorl the ribs gradually become blunt and massive. The primary ribs branch to give only two secondary ribs; no trifurcate ribs are developed. There are, however, abundant intercalatory secondary ribs, and one or two simple ribs.

The peristome is not preserved completely, but in the absence of any contrary evidence, is assumed to be simple.

Microconch. Evolute shell with a diameter of 72–112 mm. Diameter of the umbilicus 26–45 mm. The paratype has a diameter of 98 mm. and an umbilical diameter of 44 mm. It has 55 primary and 110 secondary ribs on its outer whorl. At 15 mm. diameter the paratype has 31 ribs, at 20, 33; 25, 35; 30, 36; 35, 39; 40, 40; 45, 42. The variation in rib density is shown in Text-fig. 3.

The ribs on the inner whorls are of similar style to those of the macroconch, but the point of bifurcation is somewhat lower on the whorl-side. The umbilical seam uncoils over the last half whorl.

The ribs on the last whorl gradually become coarser; occasional simple ribs are developed, and very rarely a trifurcate rib.

The peristome is straight and has a well developed ventral horn. On the paratype the horn projects 20 mm. from the venter, but it may be as short as 4 mm. The horn itself is ornamented only by growth lines, the ribs on the whorl-side fading as they approach the venter in the vicinity of the horn.

Remarks. This species is younger in age than other species of this subgenus recorded hitherto. It is distinguished by its rib-style, particularly the tendency for the ribs of the macroconch to be slightly rursiradiate. The microconch horn also tends to be free of ornamentation. On some specimens (e.g. C.73402 figured in Pl. 2, fig. 3) the venter bears scars, suggesting that earlier formed horns may have been shed.

Subgenus ***VIRGATOSPHINCTOIDES*** Neaverson 1925 : 11

1925 *Allovirgatites* Neaverson : 29.

Type species. *Virgatosphinctoides wheatleyensis* Neaverson 1925.

DIAGNOSIS. Dimorphic. Macroconchs generally finely ribbed on inner whorls. Outer whorl very variable; primary ribs strong and typically with frequent polygyrate furcation, and often a tendency to become fasciculate or virgatotome; secondary ribs obsolescent in some large species. Variocostation slight to pronounced. Peristome simple. Microconchs similarly ribbed on inner whorls to macroconchs. Body-chamber usually more coarsely ribbed than inner whorls. Peristome typically with well-developed ventral horn, more rarely only with ventrally inflated peristome. Constrictions commonly present, particularly in macroconchs.

Upper Kimmeridgian, Elegans to Hudlestoni Zones.

Pectinatites* (*Virgatosphinctoides*) *elegans sp. nov.

(Pl. 8, figs. 1*a*, 1*b*; Pl. 9)

DIAGNOSIS. Macroconchs 154–184 mm. in diameter with following rib densities: at 15 mm. diameter there are approximately 37 ribs; at 20, 38; 25, 39; 30, 39–42; 35, 40–43; 40, 41–45; 45, 42–46; 50, 43–47; 55, 44–48; 60, 45–49; 65, 46–50. Ribs slightly prorsiradiate, fairly straight. Outer whorl developing strengthened primary ribs, mainly bifurcate, but with occasional simple and polygyrate ribs and intercalatory secondaries. Microconchs 100–112 mm. in diameter with following rib densities: at 20 mm. diameter there are 39–44 ribs; at 25, 40–45; 30, 41–45; 35, 42–46; 40, 44–47. Ribs of inner whorls similar to macroconch, outer whorl slightly more strongly ribbed with occasional simple and polygyrate ribs. Peristome with ventral inflation projecting 4–8 mm.

HOLOTYPE. Macroconch C.73405.

PARATYPE (ALLOTYPE). Microconch C.73406.

MATERIAL. Fifteen specimens (six macroconchs, nine microconchs).

HORIZON. Holotype from 18 ft. and paratype from 20 ft. below the Yellow Ledge Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Elegans Zone, between 50 and 16 ft. below the Yellow Ledge Stone Band.

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 154–184 mm. Diameter of the umbilicus 65–76 mm. There are 61 primary and 137 secondary ribs on the last whorl of the holotype. At 40 mm. diameter the holotype has 45 ribs, at 45, 66; 50, 47; 55, 48; 60, 48; 65, 49; 70, 50. The variation in rib density is shown in Text-fig. 4.

The sharp dense ribs on the inner whorls are slightly prorsiradiate and straight for most of their length, but at the umbilical shoulder are rectiradiate or rursiradiate as with other species of this subgenus. The point of bifurcation of the ribs is very high on the whorl side. The umbilical seam uncoils over the last half-whorl.

The ribs on the outer whorl are similar in style to those of the inner whorls but gradually become more blunt and more widely spaced. Occasional simple and polygyrate ribs are developed on the outer whorl, but bifurcate ribs predominate.

The peristome is simple.

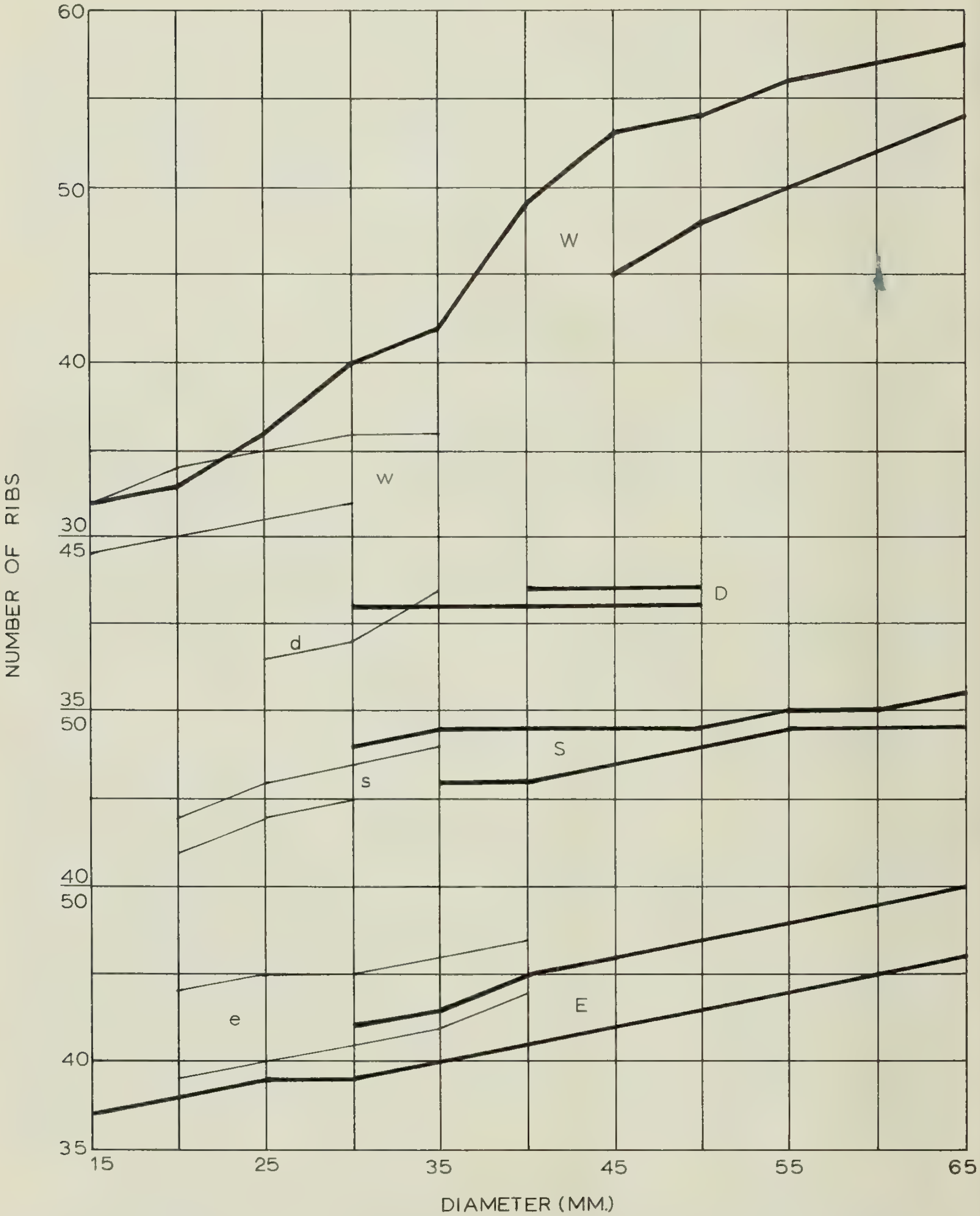


FIG. 4. Rib density of species of the subgenus *Virgatosphinctoides*. Upper case letters : macroconchs ; lower case letters : microconchs. W, w : *P.* (*V.*) *woodwardi* ; D, d : *P.* (*V.*) *decorosus* ; S, s : *P.* (*V.*) *scitulus* ; E, e : *P.* (*V.*) *elegans*.

Microconch. Evolute shell with a diameter of 100–112 mm. Diameter of the umbilicus (paratype) 40 mm. The paratype has 66 primary and approximately 130 secondary ribs on the last whorl. At 15 mm. diameter the paratype has approximately 42 ribs; at 20, 44; 25, 45; 30, 45; 35, 46; 40, 47. The variation in rib density is shown in Text-fig. 4.

The rib style of the inner whorls is very similar to that of the macroconch. The umbilical seam uncoils over the last half whorl. No suture is visible, but differences in the degree of crushing suggest that the body-chamber is half a whorl in length. The ribs on the last half whorl become slightly coarser, and occasional simple and trifurcate ribs are developed. The peristome curves forward ventrally and is inflated on the ventral margin which projects 8 mm. on the paratype. The ribs pass uninterrupted over the projection.

REMARKS. This is the earliest known species of the subgenus *Virgatosphinctoides*. The origin of the subgenus may have been from *P.* (*Arkellites*) *primitivus* described above (p. 24), the microconch of which shows a broadly similar rib style to this species, It is readily distinguished, however, by the much more finely ribbed inner whorls and the pronounced peristomal inflation. *P.* (*V.*) *elegans* is distinguished from later species of the subgenus by its rib-density, the peristomal development of the microconch and the body-chamber ornament of the macroconch.

Pectinatites* (*Virgatosphinctoides*) *elegans corniger subsp. nov.

(Pl. 10)

DIAGNOSIS. Macroconch approximately 125 mm. in diameter with following approximate rib densities: at 30 mm. 48 ribs; at 35, 49; 40, 50; 45, 51; 50, 52. Ribs prorsiradiate, fairly straight. Outer whorl developing strengthened primary ribs with fairly frequent polygyrate ribs. Microconch 82–85 mm. in diameter with following rib densities: at 20 mm. diameter approximately 43 ribs; at 25, 45; 30, 46. Inner whorls similarly ribbed to macroconch, outer whorl slightly more coarsely ribbed with occasional simple and polygyrate ribs. Peristome with ventral horn up to 7 mm. long.

HOLOTYPE. Macroconch, C.73407.

PARATYPES (ALLOTYPES). Microconchs. C.73408, C.73409.

MATERIAL. The holotype and two paratypes.

HORIZON. Holotype and paratype C.73408 from 5 ft., and paratype C.73409 from 8 ft. below the Yellow Ledge Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, topmost Elegans Zone, between 5 and 8 ft. below the Yellow Ledge Stone Band (see below).

DESCRIPTION. *Macroconch.* Evolute shell with an estimated diameter of 123 mm. Diameter of the umbilicus 50 mm. The last whorl has approximately 53 primary ribs. The number of secondary ribs cannot be determined since a part of the outer whorl has been broken away. At 39 mm. diameter there are 48 ribs; at 35, 49; 40, 50; 45, 51; 50, 52.

The ribs on the inner whorls are of a similar style to those of *P.* (*A.*) *elegans* described above but tend to be a little more prorsiradiate. The point of bifurcation of the ribs is high on the whorl side. The umbilical seam uncoils over the last half whorl. The last umbilical whorl shows the development of occasional trifurcate and simple ribs; these become more numerous on the outer whork, where there is some degree of variocostation. Over the last half whorl the primary ribs become more widely spaced and more pronounced, and there are frequent polygyrate ribs.

The peristome is not completely preserved, but is presumably simple.

Microconch. Evolute shell with a diameter of 82–85 mm. Diameter of the umbilicus 28–32 mm. There are 55–63 primary and 122–130 secondary ribs on the last whorl. At 20 mm. diameter there are 43 ribs; at 25, 45; 30, 46.

The rib style of the inner whorls is similar to that of the macroconch. The umbilical seam uncoils over the last half whorl, which appears to correspond to the length of the body-chamber, to judge by differences in the degree of crushing.

The ribs on the outer whorl are of similar style to those of the inner whorls, but become slightly coarser with the tendency to develop occasional polygyrate and simple ribs. The peristome is curved forwards dorsally, and ventrally has a horn which is 7 mm. long on paratype C.73408. The secondary ribs pass uninterrupted over the horn.

REMARKS. One fragment of an ammonite possibly belong to this subspecies was collected from the Yellow Ledge Stone Band, thus the stratigraphical range of the subspecies may extend upwards to the top of the Elegans Zone.

The subspecies is intermediate in many respects between *P.* (*V.*) *elegans* (p. 31) and *P.* (*V.*) *scitulus* (p. 34). It is intermediate in age between the two, and shows characters of both species. It is distinguished from the former species by the smaller adult size of both its macroconch and microconch, the peristomal development of the microconch, and the more strongly ribbed body chamber of the macroconch. Distinction from the latter species is based on the adult size of the macroconch and microconch, the perstomal development of the microconch, and the ribbing on the body-chamber of the macroconch which is not so markedly variocostate as in *P.* (*V.*) *scitulus*. The rib-density of the subspecies shows a closer relationship to *P.* (*V.*) *scitulus* than to *P.* (*V.*) *elegans*; however, the subspecies is assigned to the latter species because the ornament of the body-chamber of the macroconch, and the ribbed horn of the microconch show more affinity to the developments of these characters in *P.* (*V.*) *elegans*. This subspecies appears to form a direct phylogenetic link between *P.* (*V.*) *elegans* and *P.* (*V.*) *scitulus*.

Pectinatites* (*Virgatosphinctoides*) *scitulus sp. nov.

(Pl. 11)

DIAGNOSIS. Macroconchs 130–162 mm. in diameter with following rib densities: at 30 mm. diameter approximately 48 ribs; at 35, 46–49; 40, 46–49; 45, 47–49; 50, 48–49; 55, 49–50; 60, 49–50; 65, 49–51. Ribs rectiradiate to slightly prorsiradiate, straight. Outer whorl with strengthened primary ribs and variable number of simple and polygyrate ribs with occasional intercalatory secondary ribs. Microconchs 67–82 mm. in diameter with following rib densities: at 20 mm. diameter 42–44 ribs; at 25, 44–46; 30, 45–47; 35, 48. Inner whorls similar to macroconch. Outer whorl with slightly stronger ribs with tendency to be flexuous, and with occasional simple and polygyrate ribs. Peristome with feebly-ribbed ventral horn 7–16 mm. long.

HOLOTYPE. Macroconch C.73411.

PARATYPE (ALLOTYPES). Microconchs C.73412, C.73413.

MATERIAL. Twenty-two specimens (ten macroconchs, twelve microconchs).

HORIZON. Holotype from 24 ft. above the Yellow Ledge Stone Band. Paratypes from 25 and 15 ft. respectively above this band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, lower half of Scitulus Zone, occurring in the Yellow Ledge Stone Band and up to 44 ft. above this horizon.

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 130–162 mm. The holotype is 162 mm. diameter. Diameter of the umbilicus 50–78 mm. There are 47 primary and 99 secondary ribs on the last whorl of the holotype, other specimens have similar rib density on the last whorl. At 30 mm. diameter the holotype has 48 ribs; at 35, 49; 40, 49; 45, 49; 50, 49; 55, 50; 60, 50; 65, 51; 70, 52; 75, 52. The variation in the rib density is shown in Text-fig. 4.

The ribs on the inner whorls are dense and sharp. At the umbilical shoulder there is a slight rursiradial curve; the ribs then swing forwards and become straight and rectiradiate or slightly prorsiradiate. The point of bifurcation of the ribs is high on the whorl-side. The umbilical seam uncoils over the last half whorl.

The outer whorl develops coarser ribs; the primary ribs become more widely spaced, and there is the development of simple and polygyrate ribs, and intercalatory secondary ribs. There appear to be several constrictions of the shell over the last whorl, but the crushing does not allow this to be definitely ascertained. There is considerable variability in the sculpture of the outer whorl, some specimens having very frequent polygyrate ribs. The peristome is simple. The length of the body-chamber is unknown.

Microconch. Evolute shell with a diameter of 67–82 mm. Diameter of the umbilicus 25–32 mm. Paratype C.73413 has 45 primary and 92 secondary ribs on the last whorl; other specimens have similar rib density on the last whorl. At 20 mm. diameter there are 42 ribs; at 25, 44; 30, 45. Variation in rib density of the inner whorls is shown in Text-fig. 4.

The ribs on the inner whorls are identical in style to those of the macroconch. The umbilical seam uncoils over the last half whorl. Differential crushing suggest that the body-chamber varies in length from half to five-eighths of a whorl.

The outer whorl has somewhat coarser ribs which tend to be a little flexuous. At the umbilical shoulder they are rursiradiate, then swing forwards to become slightly prorsiradiate, rectiradiate, or slightly rursiradiate. There are occasional simple and polygyrate ribs on the last whorl, which may have a few constrictions.

The peristome has a ventral horn which varies in length from 7 to 16 mm. The horn is only feebly ribbed.

Remarks. The points of distinction between this species and *P.* (*V.*) *elegans* and *P.* (*V.*) *elegans corniger* have been discussed above (p. 34). It is readily distinguished from *P.* (*V.*) *decorosus* described below (p. 36) by the rib density of the inner whorls.

Pectinatites* (*Virgatosphinctoides*) *decorosus sp. nov.

(Pl. 12)

Diagnosis. Macroconchs 120–140 mm. in diameter with following rib densities: at 30 mm. diameter there are 41 ribs; at 35, 41; 40, 41–42; 45, 41–42; 50, 41–42. Ribs of inner whorls fairly straight and prorsiradiate; outer whorl developing coarser more widely spaced rectiradiate ribs, with occasional constrictions followed by simple unbranched primary rib. Microconchs approximately 85 mm. in diameter with following approximate rib densities: at 25 mm. diameter there are 38 ribs; at 30, 39; 35, 42. Inner whorls ribbed similarly to macroconch, outer whorl with stronger rectiradiate ribs, occasionally simple or polygyrate. Peristome with ventral horn up to 9 mm. long.

Holotype. Macroconch C.73414.

Paratype (allotype). C.73415.

Material. Eight specimens (four macroconchs, four microconchs).

Horizon. Holotype and paratype from 15 ft. above the Yellow Ledge Stone Band.

Stratigraphical range. Upper Kimmeridgian, Scitulus Zone, 15 to 30 ft. above the Yellow Ledge Stone Band.

Description. *Macroconch.* Evolute shell with a diameter of 120–140 mm. Diameter of the umbilicus 54–66 mm. The last whorl of the holotype has 43 primary and approximately 96 secondary ribs. At 30 mm. diameter there are 41 ribs; at 35, 41; 40, 41–42; 45, 41–42; 50, 41–42.

The ribs on the innermost whorls are very slender and delicate; they are fairly straight and slightly prorsiradiate. An initial rursiradial curve then develops at the umbilical shoulder; the ribs then swing forwards to become prorsiradiate. The point of bifurcation of the ribs is quite high on the whorl side. The umbilical seam uncoils over the last half whorl.

The ribs on the outer whorl gradually become coarser and more widely spaced, and lose most of their initial rursiradial curve to become fairly straight throughout their length. They are mainly rectiradiate, but vary from slightly rursiradiate to slightly prorsiradiate. There appear to be four or five constrictions on the outer whorl of the holotype. These are usually preceded by a polyploke rib, formed by the fusion close to the umbilical shoulder of two bifurcate ribs, and are always followed by a simple rib. Apart from these modifications, and the occasional intercalatory rib, all the ribs are bifurcate.

The peristome is simple.

Microconch. Evolute shell with a diameter of approximately 85 mm. All the measurements given are from the paratype which is the only well-preserved microconch. Diameter of the umbilicus 35 mm. The last whorl has 46 primary and approximately 90 secondary ribs. At 25 mm. diameter there are 38 ribs; at 30, 39; 35, 42.

The rib style on the inner whorls is similar to that of the macroconch. The umbilical seam uncoils over the last half whorl (which is estimated to be the length of the body-chamber). The ribs on the outer whorl are strong and rectiradiate; they are mainly bifurcate, but there are occasional simple and polygyrate ribs.

The peristome has a ventral horn of moderate length (9 mm. on the paratype) and which is ribbed. It arises gradually as an extension of the venter, and does not project very sharply as is the case in several other species of the genus.

REMARKS. The density and style of ribbing of this species render it readily distinguishable from allied species such as *P.* (*V.*) *scitulus* described above (p. 34). The rib density of the inner whorls shows some similarity to that of *P.* (*A.*) *cuddlensis* described above (p. 26), but adult size, rib style, and rib density of the outer whorl differ markedly in the two forms.

Pectinatites* (*Virgatosphinctoides*) *major sp. nov.

(Pl. 13)

DIAGNOSIS. Very large *Virgatosphinctoides* with little varicocostation. Diameter approximately 240–320 mm., with following rib densities: at 50 mm. diameter there are 42–47 ribs; at 60, 44–48; 70, 46–50; 80, 48–51; 90, 49–53; 100, 50–55; 110, 51–55; 120, 52–56; 130, 54–56; 140, 57. Ribs of inner whorls slender, rectiradiate to prorsiradiate; outer whorl with stronger rectiradiate ribs, with some simple and polygyrate ribs.

HOLOTYPE. Macroconch C.73410.

MATERIAL. Ten specimens (all macroconchs).

HORIZON. Holotype from 6 ft. below the Yellow Ledge Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Upper part of Elegans Zone and Scitulus Zone, 20 ft. below the Yellow Ledge Stone Band up to the Cattle Ledge Stone Band.

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 240–320 mm. The diameter of the umbilicus varies from 130–150 mm. The holotype is 318 mm. in diameter, has an umbilical diameter of 140 mm., and 59 primary and 124 secondary ribs on the last whorl. At 50 mm. diameter it has 46 ribs; at 55, 47; 60, 48; 65, 49; 70, 50; 75, 50; 80, 51; 85, 52; 90, 53; 95, 54; 100, 55; 105, 55; 110, 55; 115, 55; 120, 56; 125, 65; 130, 56; 135, 57; 140, 57.

The ribs on the inner whorls are slightly rursiradiate at the umbilical shoulder, and then bend forwards and become either rectiradiate or slightly prorsiradiate. The point of bifurcation of the ribs occurs fairly high on the whorl-side. The umbilical seam uncoils over the last half whorl. The length of the body-chamber is

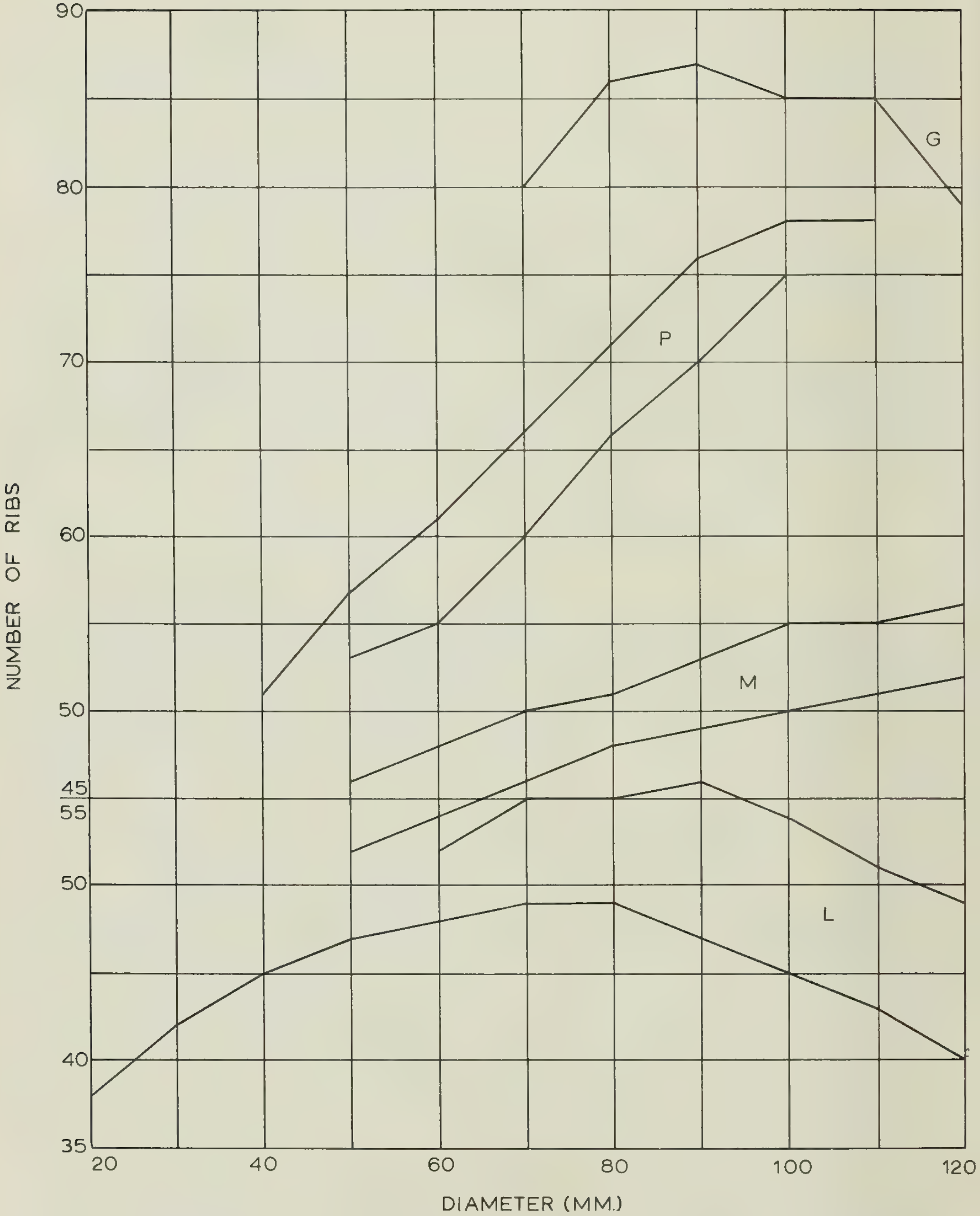


Fig. 5. Rib density of species of the subgenus *Virgatosphinctoides*. G : *P.* (*V.*) *grandis* ; P : *P.* (*V.*) *pseudoscruposus* ; M : *P.* (*V.*) *major* ; L : *P.* (*V.*) *laticostatus*.

unknown, but would appear to be greater than two-thirds of a whorl, if the differential crushing is a reliable guide. The ribs on the outer whorl gradually lose their initial rursiradial curve, and become rectiradiate throughout. There is little variocostation in this species, and the ribs of the outer whorl remain predominantly bifurcate. There are, however, occasional simple and more rarely polygyrate ribs. The holotype shows, in addition, one rib near the smooth peristome margin, which bifurcates very low on the whorl-side and again higher on the whorl, producing a total of four secondary ribs. This type of furcation (polyploke) is not seen on any other specimen of the species, otherwise the other specimens show little variation from the holotype, except that some of the specimens from higher horizons tend to develop a slightly lower point of furcation of the ribs on the body-chamber.

The microconch of this species is unknown.

REMARKS. The very large size of this species renders it readily distinguishable from other species of *Pectinatites* of the same age. It may be distinguished from other large species of the genus (all of which, described hitherto, are of younger age) by the very small degree of variocostation.

Pectinatites* (*Virgatosphinctoides*) *clavelli sp. nov.

(Pl. 14)

DIAGNOSIS. Macroconchs 210–260 mm. in diameter with following approximate rib densities: at 40 mm. diameter there are 46 ribs; at 50, 49; 60, 54–57; 70, 55–61; 80, 56–66. Ribs of inner whorls slender and rectiradiate. Outer whorl developing widely-spaced massive blunt primary ribs with frequent polygyrate furcation, and intercalatory secondary ribs. Microconchs 67–87 mm. diameter with following rib densities: at 25 mm. diameter there are 42 ribs; at 30, 43–44; 35, 44. Inner whorls similarly ribbed to macroconch. Outer whorls somewhat more coarsely-ribbed with occasional polygyrate and simple ribs. Peristome projecting ventrally by up to 5 mm.

HOLOTYPE. Macroconch C.73432.

PARATYPES (ALLOTYPES). Two microconchs, C.73433, C.73434.

MATERIAL. Eleven specimens, all plaster casts (five macroconchs, six microconchs).

HORIZON. Holotype from 8 ft., and paratypes from 3 ft. above the Grey Ledge Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, lower Wheatleyensis Zone, between 3 and 28 ft. above the Grey Ledge Stone Band.

DESCRIPTION. *Macroconch.* Large evolute shell with a diameter of approximately 210–260 mm. The diameter of the umbilicus varies from 104 to 130 mm.

The last whorl of the holotype which is 212 mm. in diameter has 51 primary and an estimated 122 secondary ribs. The innermost whorls are not completely preserved in any one specimen. At 60 mm. diameter the holotype has 57 ribs, at 70, 62; 80, 66; 90, 69; 100, 71. The variation in rib density is shown in Text-fig. 6.

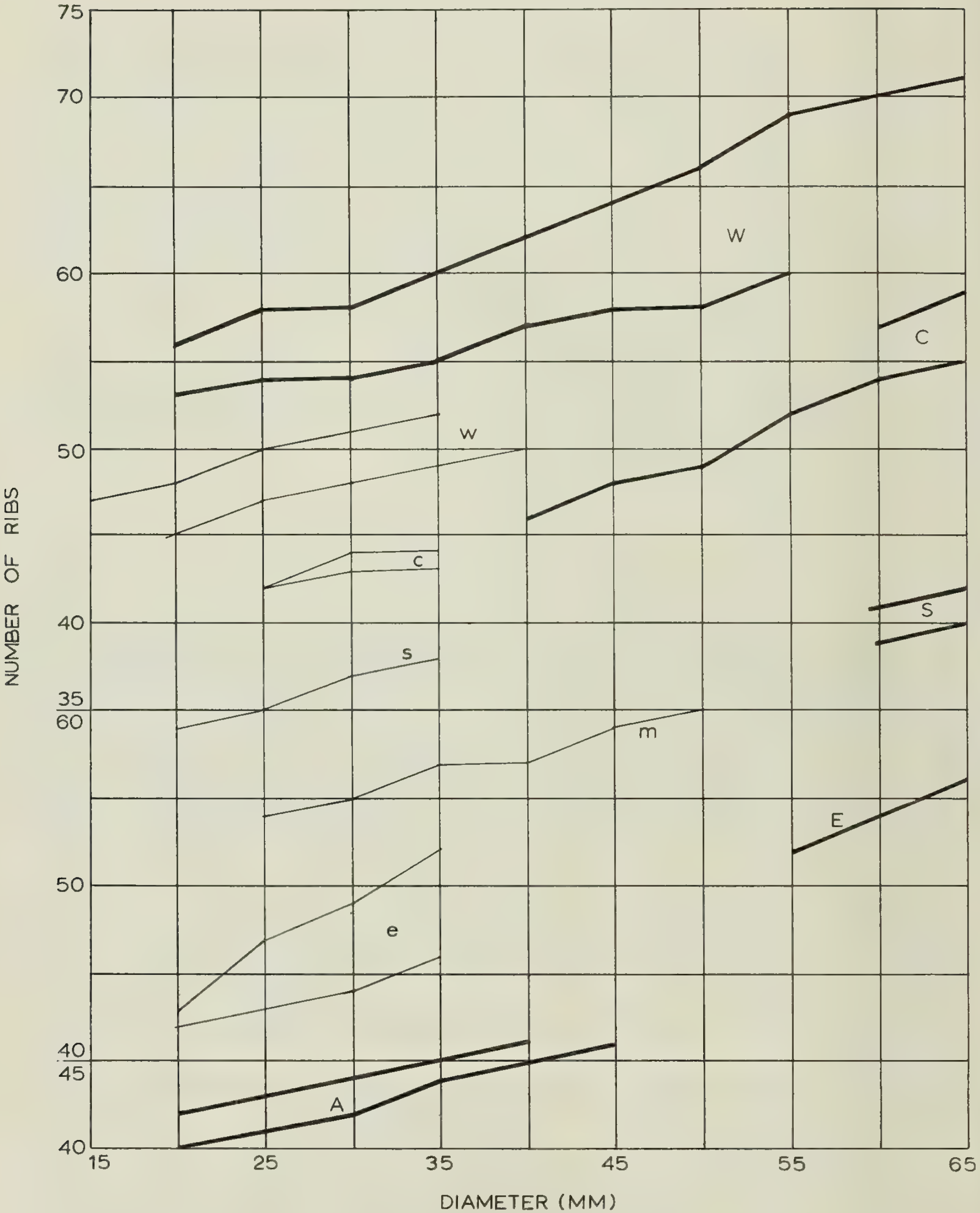


FIG. 6. Rib density of species of the subgenus *Virgatosphinctoides*. Upper case letters : macroconchs ; lower case letters : microconchs. W, w : *P.* (*V.*) *wheatleyensis* ; C, c : *P.* (*V.*) *clavelli* ; S, s : *P.* (*V.*) *smedmorensis* ; m : *P.* (*V.*) *magnimasculus* ; E, e : *P.* (*V.*) *encombensis* ; A : *P.* (*V.*) *abbreviatus*.

The ribs on the inner whorl are rursiradiate at the umbilical shoulder; they then swing forwards and become straight and more or less rectiradiate. The point of bifurcation of the ribs is high on the whorl-side. There is a marked uncoiling of the umbilical seam over the last half whorl.

The ribs on the outer whorl become coarser, and the primary ribs become more widely spaced and irregular in their style and furcation. Some are rursiradiate, others rectiradiate or prorsiradiate. Several of the primary ribs show polygyrate furcation, and there is also a profusion of simple and intercalatory ribs on the last whorl.

The peristome is simple.

Microconch. Evolute shell considerably smaller than the macroconch, having a diameter of only 68–87 mm. The diameter of the umbilicus is 30–37 mm. There are 46 primary and 94 secondary ribs on the last whorl of paratype C .73434. The rib style of the inner whorls is similar to that of the macroconch. At 25 mm. diameter there are 42 ribs; at 30, 43–44; at 35, 44. (Text-fig. 6).

The point of bifurcation of the ribs is high on the whorl-side. The umbilical seam uncoils noticeably over the last half whorl.

The outer whorls of both specimens are rather distorted by the crushing so that it is not easy to deterine the original rib direction. It would appear, however, to be rursiradiate at the umbilical shoulder, then becoming straight and rectiradiate. There are occasional simple ribs on the last whorl and a few primary ribs with three, or in one case, four secondary ribs.

The ventral part of the perstome bears a short ribbed horn 4–5 mm. in length. It arises gradually from the venter and is not well preserved on either paratype.

REMARKS. The adult diameter of the macroconch and microconch, their rib density, and the development of the microconch horn, serve to distinguish this species from others. *P.* (*V.*) *smedmorensis* described below is considerably more coarsely ribbed than this species. As the highest beds of the underlying Scitulus Zone have hitherto yielded no ammonites, it is not possible to determine the origin of this species. The degree of variocostation of the macroconch is more pronounced than that of *P.* (*V.*) *scitulus*, but the general rib style of the two species shows some similarities. The very irregular costation of the body-chamber of the macroconch is a feature characteristic of many of the younger species of the subgenus *Virgatosphinctoides*. The development of the microconch horn in this species is not, however, very typical.

Pectinatites* (*Virgatosphinctoides*) *smedmorensis sp. nov.

(Pl. 15, figs. 1, 2)

DIAGNOSIS. Macroconchs approximately 150 mm. in diameter with following approximate rib densities: at 60 mm. diameter there are 39–41 ribs; at 65, 39–41; 70, 40–42; 75, 41–43; 80, 42. Ribs on inner whorls slender and prorsiradiate becoming rursiradiate with strengthening of primary ribs on body-chamber. Polygyrate, simple and intercalatory secondary ribs occur occasionally. Constrictions developed over last two whorls. Microconchs 86–107 mm. in diameter with following approximate rib-densities: at 20 mm. diameter there are 34 ribs; at 25, 25; 30, 27; 35, 38. Ribs of inner whorls similar in style to macroconch, becoming a little coarser on outer whorl. Peristome bearing ventral horn up to 8 mm. long.

HOLOTYPE. Macroconch, plaster cast C·73430.

PARATYPE (ALLOTYPE). Microconch, plaster case C·73431.

MATERIAL. Five specimens, including three macroconchs (two of which are plaster casts, and two microconchs (both plaster casts)).

HORIZON. Both type specimens are from 22 ft. below the Blackstone.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, lower Wheatleyensis Zone, from 8 ft. above the Grey Ledge Stone Band, to 22 ft. below the Blackstone (A vertical range of 41 ft.).

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of approximately 150 mm. Diameter of the umbilicus approximately 85 mm. At 60 mm. diameter the holotype has 39 ribs; at 65, 39; 70, 40; 75, 41; 80, 42. (Text-fig. 6).

The ribs on the inner whorls are rectiradiate at the umbilical shoulder, then swing forwards to become fairly straight and prorsiradiate. The point of bifurcation of the ribs is fairly high on the whorl-side. The umbilical seam uncoils over the last half to three-quarters of a whorl.

The ribs on the outer whorl gradually lose their prorsiradiate tendency and become straight and slightly rursiradiate throughout their length. The primary ribs become more widely spaced and very sharp, and the development of the secondary ribs becomes irregular. There are occasional polygyrate, simple and intercalatory ribs.

There are several constrictions present. On the last half-whorl these are straight and are followed by a simple rib. The constrictions developed earlier are quite pronouncedly prorsiradiate, however. These oblique constrictions are preceded by a trifurcate rib which branches low on the whorl-side, and are followed by a simple rib.

A part of the suture line is present on one specimen; it is not well-preserved, however, but does show stout saddles and lobes. Both lateral lobes appear to be trifid.

The peristome is not completely preserved on any specimen but is presumably simple.

Microconch. Neither microconch is particularly well or completely preserved. Both specimens are plaster casts. The paratype is quite evolute and has a diameter of 86 mm. The diameter of the umbilicus is 36 mm. There are an estimated 46 primary ribs on the last whorl.

The ribs of the inner whorls are similar in style to those of the macroconch. At 20 mm. diameter there are 34 ribs; at 25, 35; 30, 37; 35, 38. (Text-fig. 6).

The outer whorl has ribs of similar style, but they become a little coarser. There is one possible constriction present at the aperture.

The ventral part of the peristome is damaged, but there is visible the basal 3 mm. of a horn, the original length of which may have been 7–8 mm.

REMARKS. Most characters of this species are sufficiently distinctive to separate it from other species. It is distinguished from *P.* (*V.*) *clavelli* described above (p. 39) by the smaller adult size of the macroconch and the more coarsely-ribbed inner whorls. The microconch has a similar rib-density on its inner whorls to that of *P.* (*V.*) *woodwardi* (p. 45), but may be distinguished by the rib-style of both inner and outer whorls.

Pectinatites* (*Virgatosphinctoides*) *laticostatus sp. nov.

(Pl. 16)

DIAGNOSIS. Large *Virgatosphinctoides* developing massive widely-spaced primary ribs over last two whorls. Diameter 230–320 mm., with following approximate rib densities: at 20 mm. diameter there are 38 ribs; at 30, 42; 40, 45; 50, 47; 60, 48–52; 70, 49–55; 80, 49–55; 90, 47–56; 100, 45–53; 110, 43–51; 120, 40–49 130, 38–45. Ribs of inner whorls rectiradiate to prorsiradiate becoming more widely spaced from ante-penultimate whorl onwards. Outer whorl extremely coarsely ribbed with abundant intercalatory secondary ribs. Microconch unknown.

HOLOTYPE. Plaster cast C.73416.

MATERIAL. Six specimens, including two plaster casts (all macroconchs).

HORIZON. Holotype from " dicey " shales 19 ft. below the Blackstone.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, lower Wheatleyensis Zone ranging from 3 ft. above the Grey Ledge Stone Band to 13 ft. 6 in. below the Blackstone (a vertical range of 47 ft.).

DESCRIPTION. Large evolute shell with a diameter of 232–320 mm. Diameter of umbilicus 130–180 mm. The holotype has 27 primary and approximately 68 secondary ribs on the last whorl. At 20 mm. diameter holotype has approximately 38 ribs; at 30, 42; 40, 45; 50, 47; 60, 48; 70, 49; 80, 49; 90, 47; 100, 45; 110, 43; 120, 40; 130, 38. The variation in rib density is shown in Text-fig. 5.

The ribs on the innermost whorls are rursiradiate at the umbilical shoulder then swing forwards to become rectiradiate or slightly prorsiradiate. A coarsening of the ribs develops very early, and the last three whorls become progressively more coarsely ribbed. There is a gradual loss of the initial rursiradial curve of the ribs and they become straight throughout their length. The point of bifurcation of the ribs is high on the whorl-side, and the angle of furcation is somewhat larger (at least on the outer whorls), than is usual in this subgenus. The umbilical seam uncoils over the last half whorl.

The outer whorl becomes extremely coarsely ribbed and abundant intercalatory secondary ribs are developed.

At least two constrictions are present on the holotype, one on the penultimate and one on the antepenultimate whorl; they are both strongly oblique. In each case the constriction is preceded by a biplicate rib, which branches very close to the umbilical shoulder. A simple rib follows the constriction.

The peristome is not preserved intact on the holotype, but is presumed to be simple. The microconch of this species has not been found hitherto.

Remarks. The very early development of widely-spaced ribs in this species is an uncommon character in this subgenus, and is therefore a very useful character for identification of this species. The problematical *Virgatosphinctoides nodiferus* Neaverson (1925 : 14, pl. 4, fig. 1) has a similar style of ribbing on its outer whorl, but its rib-development is not known in any detail. It is apparently geologically younger than *P.* (*V.*) *laticostatus*.

Pectinatites* (*Virgatosphinctoides*) *grandis (Neaverson)

(Pl. 15, fig. 3; Pl. 18)

1925 *Virgatosphinctoides grandis* Neaverson : 13, pl. 4, fig. 2.

Material. Eight specimens; seven macroconchs, one possible microconch.

Stratigraphical range. Upper Kimmeridgian, upper part of Wheatleyensis Zone, between 3 and 17 ft. below the Blackstone.

Description. *Macroconch.* There is good agreement between one of the specimens here figured (Pl. 18) and the holotype, which came from Corton, Dorset. The former has a diameter of 365 mm. The umbilicus has a diameter of 168 mm. There are 24 primary and approximately 82 secondary ribs on the last whorl. At 80 mm. diameter there are 86 ribs, at 90, 87; 100, 85; 110, 85; 120, 79; 130, 77; 140, 71; 150, 68; 160, 64. The variation in rib-density of the Kimmeridge forms is shown in Text-fig. 5.

The ribs on the inner whorls are rursiradiate at the umbilical shoulder and gradually swing forwards, so that less than half way up the whorl-side they become prorsiradiate. On the last umbilical whorl the ribs become more widely spaced, until on the outer whorl the primary ribs are very strong and distant from one another.

There are often large numbers of secondary ribs to each primary rib. On some specimens there are regularly as many as five secondary ribs to each primary rib. The ribs become straighter on the last part of the body-chamber and slightly prorsiradiate throughout their length. The secondary ribs tend to become less prominent and several primary ribs may be unbranched. Some intercalatory secondary ribs are usually present on the last whorl. There are several constrictions present. They are preceded by a compound rib, and followed by a simple rib.

The peristome is presumably simple.

Microconch. The figured microconch comes from the same horizon (17 ft. below the Blackstone) as the earliest recorded macroconch of this species.

It is 112 mm. in diameter. The diameter of the umbilicus is 45 mm. There are approximately 70 primary ribs on the last whorl. At 40 mm. diameter there are approximately 68 ribs. The ribs of the inner whorl are similar in style to those of macroconch. The outer whorl is similarly ribbed, but has occasional simple and polygyrate ribs and at least one constriction. The aperture bears a horn which projects from the venter by about 7 mm.

Remarks. There is a great disparity in size between the microconch (112 mm. diameter) and the associated macroconch (approximately 280 mm. diameter). However, it has been found that as a general rule the microconch is usually slightly coarser-ribbed than its macroconch at the same diameter. In this case the microconch has 68 ribs at 45 mm. diameter while the macroconch has approximately 70 at this diameter. No other fine-ribbed macroconchs occur at this horizon, so that there can be little doubt that this specimen is the microconch of *P.* (*V.*) *grandis.*

The size of this species, coupled together with rib-style and density distinguish it from other species of the genus.

Pectinatites* (*Virgatosphinctoides*) *grandis acceleratus subsp. nov.

(Pl. 19)

DIAGNOSIS. Very large *Virgatosphinctoides.* General characters similar to *P.* (*V.*) *grandis* (Neaverson) but development of modified ornament occurring earlier. Ribs of outer whorl blunt and massive with few secondaries. Some intercalatory secondary ribs.

HOLOTYPE. Macroconch C.73422, the only specimen.

HORIZON. 13 ft. above the Rope Lake Head Stone Band. (Upper Kimmeridgian, basal part of Hudlestoni Zone).

DESCRIPTION. Large evolute shell with a diameter of approximately 375 mm. Diameter of the umbilicus 175 mm. There are 23 primary and approximately 60 secondary ribs on the last whorl.

This subspecies is similar in most respects to *P.* (*V.*) *grandis* described above. It differs in that it becomes coarser-ribbed earlier in development, but the different types of sculpture present in *P.* (*V.*) *grandis* are repeated in the same order, but at smaller diameters.

The peristome is simple.

REMARKS. This subspecies is closely related to *P.* (*V.*) *grandis* and must be interpreted as a direct derivative of it. There is, however, a thickness of approximately 35 ft. of rock between the highest recorded occurrence of *P.* (*V.*) *grandis* and the horizon from which this subspecies came. Most of the intervening rocks, however, are extremely poorly fossiliferous, so that collection failure is most probably responsible for the " break ".

No microconch of this subspecies has been found hitherto.

Pectinatites* (*Virgatosphinctoides*) *woodwardi (Neaverson)

(Pl. 20)

1925 *Allovirgatites woodwardi* Neaverson : 31, pl. 3, fig. 1.
1925 *Allovirgatites robustus* Neaverson : 32, pl. 3, fig. 3.
1925 *Allovirgatites versicostatus* Neaverson : 32, pl. 3, fig. 4.
1926 *Allovirgatites woodwardi* Neaverson ; Buckman, pl. 637.

MATERIAL. Eleven specimens (five macroconchs, six microconchs).

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Wheatleyensis Zone (just above the middle), ranging between 15 and 9 ft. below the Blackstone.

Description. *Macroconch.* Fairly evolute shell with a diameter of 150–185 mm. Diameter of umbilicus 74–88 mm. The last whorl of the specimen here figured which is approximately 155 mm. diameter has an estimated 46 primary and 111 secondary ribs. The innermost whorls are not completely preserved in any specimen. At 50 mm. diameter there are 49 ribs, at 55, 52; 60, 54; 65, 55; 70, 56. (Text-fig. 4).

The ribs on the inner whorls are rursiradiate at the umbilical shoulder, then swing forwards to become rectiradiate or slightly prorsiradiate and more or less straight. The point of bifurcation of the ribs is high on the whorl-side.

The umbilical seam uncoils over the last half-whorl. (This uncoiling is not noticeable in the plate reproduced herein, owing to the crushing of the last umbilical whorl which gives an incorrect impression of the amount of this whorl exposed.)

The ribs on the outer whorl become more widely spaced and stouter. The point of furcation is sometimes lower on the whorl-side. The number of secondary ribs per primary is variable, with as many as four secondary ribs to each primary rib. There are at least two possible constrictions on the outer whorl. The peristome is not preserved intact on any specimens, but is presumably simple.

Microconch. Fairly evolute shell with a diameter of approximately 68–77 mm. The diameter of the umbilicus is 25–30 mm. The figured specimen has 49 primary and an estimated 92 secondary ribs on its last whorl. At 20 mm. diameter there are approximately 34 ribs; at 25, 35; 30, 36. The variation in rib density is shown in Text-fig. 4.

The inner whorls are similar in rib style to those of the macroconch. The umbilical seam uncoils over the last half whorl (not well-shown on the figured microconch).

The ribs of the outer whorl lose most of their initial rursiradial curve and are almost straight and rectiradiate. There is some slight variability in the rib direction, however, from slightly rursiradiate to slightly prorsiradiate. There are occasional simple and trifurcate ribs on the last whorl.

The peristome is not preserved intact on any one specimen. The figured specimen shows it to be more or less straight, however. The ventral part of the peristome on this specimen projects about 2 mm. and is then broken, so that it is safe to conclude that a horn was originally present.

Remarks. The Dorset specimens agree closely with Neaverson's figure of *Allovirgatites woodwardi*. *A. robustus* Neaverson is merely an incomplete specimen of the same species, apparently a little thicker-whorled, but still very close to the former species. *A. versicostatus* Neaverson is also very close to this species and may possibly be the microconch. The differences do not appear to be sufficient to warrant specific distinction. The association of *P.* (*V.*) *woodwardi* with *P.* (*V.*) *wheatleyensis* (Neaverson) is also indicative of the similarity of the Dorset to the Oxford material.

Pectinatites* (*Virgatosphinctoides*) *wheatleyensis Neaverson

(Pl. 21)

1925 *Virgatosphinctoides wheatleyensis* Neaverson : 12, pl. 1, fig. 1.
1956 *Subplanites* (*Virgatosphinctoides*) *wheatleyensis* (Neaverson) Arkell : 779, pl. 40, fig. 1.

Material. Eleven specimens (five macroconchs, six microconchs).

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Wheatleyensis Zone (just above the middle), ranging from 15 to 9 ft. below the Blackstone.

DESCRIPTION. *Macroconch.* One specimen from Kimmeridge here figured, (Pl. 21, fig. 1) agrees extremely closely with the holotype figured by Neaverson. It has a diameter of 132 mm. The diameter of the umbilicus is 57 mm. There are approximately 64 primary and 156 secondary ribs on the last whorl. Another specimen, which has well preserved inner whorls, has rib density as follows: at 25 mm. diameter there are 54 ribs, 30, 54; 35, 55; 40, 57; 45, 58; 50, 58; 55, 60. The variation in rib density of the Kimmeridge specimens is shown in Text-fig. 6.

The ribs on the inner whorls are rursiradiate at the umbilical shoulder, then swing forwards to become rectiradiate or slightly prorsiradiate. The point of bifurcation of the ribs is high on the whorl-side. The umbilical seam uncoils on the last half whorl.

The outer whorl is very variable. The primary ribs become more widely spaced and are mostly polygyrate in some specimens. Others show the persistence of a more conservative type of ribbing, with more bifurcate than polygyrate ribs.

One specimen shows the last few approximated suture lines, but as these are extremely poorly preserved, comparison with the suture line figured by Neaverson (1925, text-fig. B, 5) is not possible. However, it can be seen from these suture lines that the body-chamber is half a whorl in length.

The peristome is simple and straight.

Microconch. One specimen figured herein (C. 73426) has a diameter of 91 mm. The diameter of the umbilicus (which is somewhat elongated by crushing) is 36 mm. There are 56 primary and 122 secondary ribs on the last whorl. The inner whorls are badly preserved, so that it is not possible to determine the rib density accurately. There are, however, approximately 50 ribs at 35 mm. diameter. The other figured specimen (C. 73427) has at 15 mm. diameter 47 ribs, at 20, 47; 25, 48; 30, 49. (Text-fig. 6).

The ribs on the inner whorls are of a similar style to the macroconch. The umbilical seam uncoils over the last half whorl (which appears to correspond to the length of the body-chamber).

The ribs on the outer whorl become slightly coarser, and there is the development of occasional polygyrate and simple ribs.

The peristome bears a horn when completely preserved, and this is 17 mm. long on specimen C. 73426. It is quite strongly ribbed.

REMARKS. The horizon at which this species occurs in Dorset is much lower than that quoted by Arkell (1947 : 71). Although the ammonites from just below the Basalt Stone Band are undoubtedly somewhat similar in appearance to this species, the outer whorls are not the same. The associated fauna also confirms the identity of this species. Neaverson placed his Wheatleyensis Zone immediately above the *Gravesia* Zones, which is too low in the succession.

Pectinatites* (*Virgatosphinctoides*) *wheatleyensis minor subsp. nov.

(Pl. 24, fig. 1)

DIAGNOSIS. Macroconchs small (103–108 mm. diameter) with following approximate rib densities: at 25 mm. diameter there are 44 ribs; at 30, 48; 35, 46; 40, 48; 45, 49. Ribs of inner whorls slender and approximately rectiradiate. Outer whorl developing strengthened primary ribs, remaining approximated, with polygyrate furcation predominant.

Holotype. Macroconch C.73429.

Material. Two specimens (both macroconchs).

Horizon. Both specimens from 17 ft. below the Blackstone (Upper Kimmeridgian, middle Wheatleyensis Zone).

Description. Evolute shell with a diameter of 103–108 mm. (small for a macroconch). Diameter of umbilicus 43–45 mm. There are approximately 53 primary and 144 secondary ribs on the last whorl. In rib style this subspecies is very similar to *P.* (*V.*) *wheatleyensis*, but is somewhat more coarsely ribbed. At 20 mm. diameter there are approximately 44 ribs, at 30, 45; 35, 46; 40, 48; 45, 49. The point of bifurcation of the ribs is high on the whorl-side. The umbilical seam uncoils over the last half-whorl. The ribs on the outer whorl are identical in style with those of the holotype of *P.* (*V.*) *wheatleyensis*, being mostly polygyrate.

The peristome is simple.

Remarks. The microconch of this subspecies is not known. Apart from the somewhat more coarsely ribbed inner whorls, and smaller adult size, this subspecies is similar to *P.* (*V.*) *wheatleyensis*. Its lower stratigraphical horizon suggests that it is a possible ancestor of this species.

Pectinatites* (*Virgatosphinctoides*) *wheatleyensis delicatulus (Neaverson)

(Pl. 27, fig. 2)

1925 *Virgatosphinctoides delicatulus* Neaverson : 15, pl. 1, figs. 2 and ?3.
1925 *Allovirgatites tutcheri* Neaverson : 30, pl. 3, fig. 2.
1926 *Allovirgatites tutcheri* Neaverson ; Buckman, pl. 692.

Material. Five specimens (four macroconchs, one possible microconch).

Stratigraphical range. Upper Kimmeridgian, Wheatleyensis Zone (upper part) between 7 and 4 ft. below the Blackstone (see below).

Description. *Macroconch.* The Dorset specimens agree closely with Neaverson's figure of the holotype, but are complete individuals. One specimen with a diameter of approximately 130 mm. and an umbilical diameter of 53 mm. has about 78 primary and 151 secondary ribs on the last whorl. The ribs on the inner whorl are a little finer and more dense than those of *P.* (*V.*) *wheatleyensis*. Some specimens have several constrictions of the last umbilical and the outer whorl.

The main point of difference between this subspecies and *P.* (*V.*) *wheatleyensis* lies in the more finely ribbed outer whorl, and the constrictions which are usually present. The constrictions are preceded by a polygyrate or polyploke rib and are followed by a simple rib. In some cases this rib is prominent like the flare of *Lytoceras*. (As is the case with Neaverson's examples).

The peristome is simple. The body-chamber is a half whorl in length.

Microconch. A single poorly preserved specimen from 5 ft. below the Blackstone is possibly the microconch of this subspecies. It is 91 mm. in diameter, has an umbilical diameter of 35 mm. and has approximately 56 primary and 112 secondary ribs on the last whorl. The inner whorls are so hidden by pyrite aggregates, however, that it cannot be with certainty referred to this subspecies.

The umbilical seam uncoils over the last half whorl. The peristome is missing, but was presumably originally horned.

REMARKS. *Allovirgatites tutcheri* Neaverson differs from *Virgatosphinctoides delicatulus* Neaverson by no more than the difference between two individuals of the same species. The general similarity to *P.* (*V.*) *wheatleyensis* justifies separation only at subspecific level.

This subspecies, which is stratigraphically a little younger than *P.* (*V.*) *wheatleyensis*, is certainly a derivative of it. One specimen which I refer to *P.* (*V.*) *wheatleyensis* is similarly ribbed to this subspecies on the inner whorls, but is intermediate between the two forms in the ribbing of its outer whorl.

Several very poorly preserved ammonites from the shales 4–10 ft. above the Blackstone are provisionally included in this subspecies.

Pectinatites* (*Virgatosphinctoides*) *pseudoscruposus (Spath)

(Pl. 17)

1936 *Subplanites pseudoscruposus* Spath : 173, fig. 2.
1947 *Subplanites pseudoscruposus* Spath ; Arkell : 77, fig. 17, 1.

EMENDED DIAGNOSIS. Diameter of shell 220–230 mm. with following rib densities: at 40 mm. diameter there are approximately 51 ribs; at 50, 53–57; 60, 55–61; 70, 60–66; 80, 66–71; 90, 70–76; 100, 75–78. Ribs on inner whorls slender and prorsiradiate. Outer whorl developing massive blunt primary ribs typically with virgatotome furcation, with up to six secondary ribs to each primary.

MATERIAL. Six specimens (all macroconchs).

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Wheatleyensis Zone (upper part), between 9 and 3 ft. below the Blackstone.

DESCRIPTION. Large evolute shell with a diameter of 220 to approximately 230 mm. Diameter of umbilicus 110–115 mm. The specimen figured herein (C.73418) has 36 primary and approximately 104 secondary ribs on the last whorl (about one-eighth of a whorl is missing).

At 50 mm. diameter this specimen has 57 ribs, at 60, 59; 70, 66; 80, 72; 90, 76; 100, 77; 110, 78. The variation in rib density is shown in Text-fig. 5.

The ribs on the inner whorls are fine and slender. They are curved rursiradially at the umbilical shoulder, but swing forwards rapidly to become prorsiradiate and almost straight. The point of bifurcation of the ribs is high on the whorl-side. The umbilical seam uncoils over the last half to three-quarters of a whorl.

The sculpture of the outer whorl is extremely variable, no two specimens being alike in this respect. Typically there are developed very prominent blunt primary ribs which tend to become virgatotome, with up to six secondary ribs. There are occasional simple and intercalatory secondary ribs.

Constrictions are also present on the last whorl of some specimens of this species. These are preceded by a virgatotome rib with four or five secondary ribs, and are followed by a simple rib.

The microconch of this species is unknown.

REMARKS. The validity of this species may be questioned, as it does not entirely fulfil the requirements of Article 13 of the International Code of Zoological Nomenclature. However, the outer whorl fragment upon which Spath based this species is absolutely characteristic and there can be no doubt of its interpretation. Spath's figure is misleading in that the inner whorls he associated with the outer whorl fragment almost certainly belong to a different species. The name of this species is well-known to those familiar with British Kimmeridgian ammonites, and there would seem to be little to be gained by rejecting a name because its original description was legally defective. The intention here has been to give a more satisfactory definition of the species by figuring a more complete specimen and giving a comprehensive description.

Pectinatites (Virgatosphinctoides) reisiformis sp. nov.

(Pl. 22; Pl. 23, fig. 3)

DIAGNOSIS. Macroconchs 155–255 mm. in diameter with following rib densities: at 20 mm. diameter there are 48–52 ribs, at 25, 49–54; 30, 52–56; 35, 54–58; 40 55–58; 45, 56–59; 50, 57–61; 55, 58–63; 60, 59–64; 65, 60–65; 70, 61–66. Ribs of inner whorls slender and prorsiradiate. Outer whorl becoming suddenly more coarsely-ribbed with polygyrate then virgatotome ribs, with abundant simple and intercalatory secondary ribs. Microconchs 78–110 mm. in diameter with following rib densities: at 20 mm. diameter there are approximately 42 ribs; at 25, 42–44; 30, 43–46; 35, 44–47; 40, 46–49; 45, 48–52. Ribs of inner whorls similar to macroconch. Outer whorl more coarsely ribbed with occasional simple and polygyrate ribs and intercalatory secondaries. Peristome with ventral horn 10–20 mm long.

HOLOTYPE. Macroconch C.73435.

PARATYPE (ALLOTYPE). Microconch C.73436.

MATERIAL. Twenty-five specimens (seventeen macroconchs, eight microconchs).

HORIZON. Both holotype and paratype are from shales 13 ft. above the Rope Lake Head Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, uppermost Wheatleyensis and basal Hudlestoni Zones, from 6 ft. above the Blackstone to 16 ft. above the Rope Lake Head Stone Band.

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 155–255 mm. Diameter of umbilicus 65–118 mm. The holotype has a diameter of 174 mm., and an umbilical diameter of 76 mm. There are 51 primary and 118 secondary ribs on

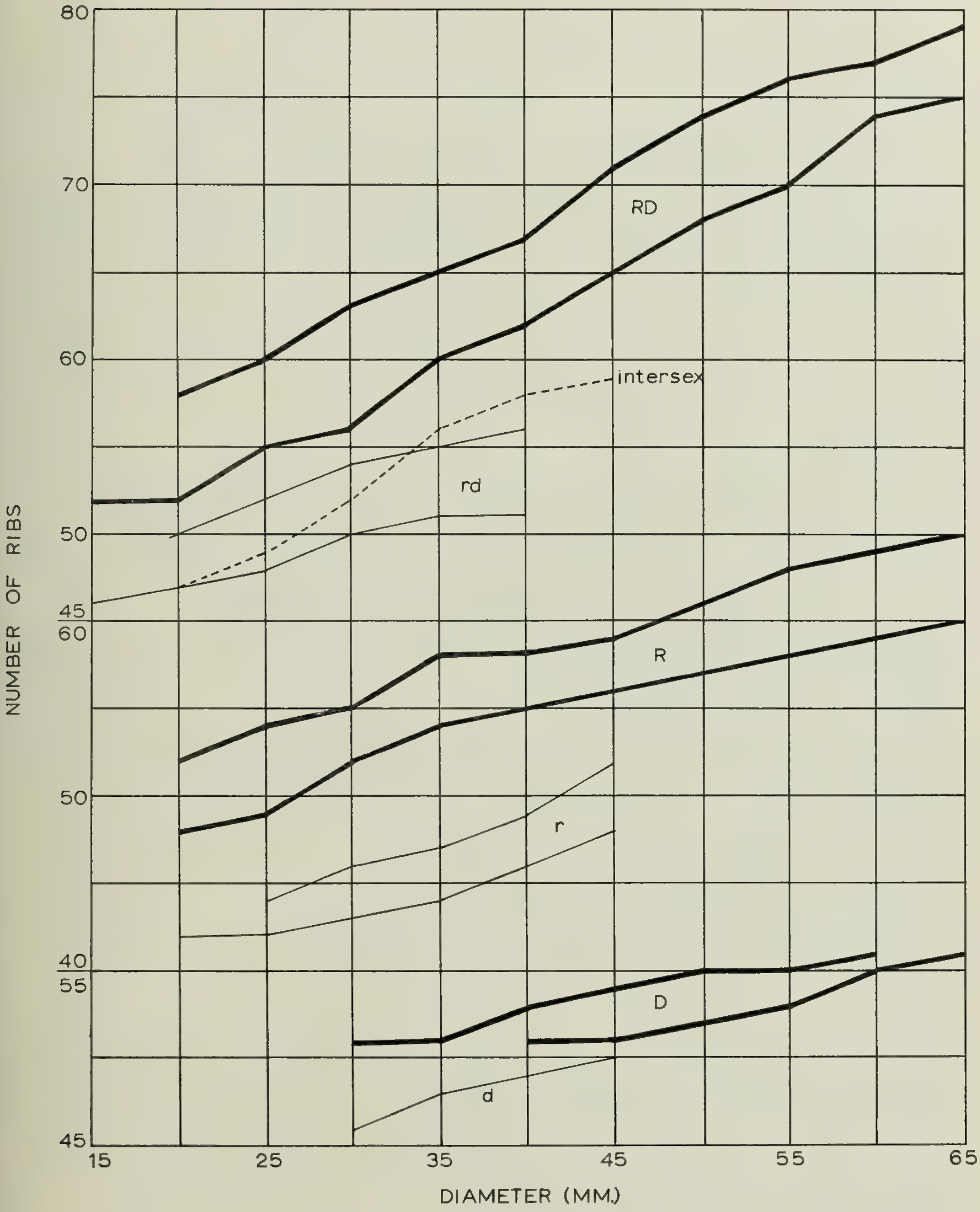


FIG. 7. Rib density of species of the subgenus *Virgatosphinctoides*. Upper case letters: macroconchs; lower case letters: microconchs. RD, rd: *P.* (*V.*) *reisiformis densicostatus*; R, r: *P.* (*V.*) *reisiformis*; D, d: *P.* (*V.*) *donovani*.

the last whorl. The inner whorls are well preserved on the holotype. At 20 mm. diameter there are 48 ribs, at 25, 49; 30, 52; 35, 54; 40, 55; 45, 56; 50, 57; 55, 58; 60, 59; 65, 60; 70, 61; 75, 62. The variation in rib density is shown in Text-fig. 7.

The ribs on the inner whorls are dense and slender. They are rursiradiate at the umbilical shoulder, then swing forwards to become prorsiradiate (pronouncedly so in some specimens). The point of bifurcation of the ribs is high on the whorl-side. The umbilical seam uncoils over the last half to three-quarters of a whorl.

On the outer whorl the ribs become rather suddenly more widely spaced. At first, polygyrate ribs are developed; then as the primary ribs become stouter and blunter, the branching has a tendency towards the virgatotome condition, with up to four secondary ribs to each primary rib. There are abundant simple and intercalatory ribs on the last whorl.

The ribbing of the outer whorl is extremely variable in this species. No two specimens are alike in this respect. Some of the larger specimens are obviously gerontic individuals, the last secreted half whorl or so of their shell being almost devoid of ornament.

The peristome is not preserved on the holotype, but other specimens show it to be straight and simple.

Microconch. Evolute shell with a diameter of 78–110 mm. The diameter of the umbilicus varies from 30–42 mm. The paratype is 110 mm. in diameter and has an umbilical diameter of 42 mm. There are 63 primary and 126 secondary ribs on the last whorl of the paratype. At 25 mm. diameter the paratype has 44 ribs, at 30, 45; 35, 47; 40, 48. The variation in rib density is shown in Text-fig. 7.

The ribs of the inner whorls are similar in style to those of the macroconch, but tend not to be so markedly prorsiradiate. The point of bifurcation of the ribs is a little lower on the whorlside than on the macroconchs. The umbilical seam uncoils over the last half whorl.

The outer whorl becomes more coarsely ribbed, and there is a tendency for the ribs to become somewhat flexuous. At, or just below the point of furcation, the ribs bend back a little. This feature is well shown on the paratype. Almost all the ribs on the outer whorl are bifurcate, but there are very occasional simple, polygyrate, and intercalatory ribs.

The peristome is somewhat sinuous, and laterally extends anteriorly a little. There is a well developed ventral horn, which is often feebly ribbed. On the paratype the horn projects from the venter by about 18 mm. In some specimens growth has proceeded a little beyond the horn; this anteriorly extended portion of the shell shows little or no ornamentation.

REMARKS. The density of the ribbing on the inner whorls, and the sculpture of the outer whorl are distinctive features of this species. It may be derived from *P.* (*V.*) *wheatleyensis* but shows considerably more variocostation than this latter species. The diversity of the ornamentation of the body-chamber of the macroconchs contrasts with the rib-density of the inner whorls which are remarkably similar in rib style and density.

Pectinatites* (*Virgatosphinctoides*) *reisiformis densicostatus subsp. nov.

(Pl. 23, figs. 1, 2; Pl. 24, fig. 2)

DIAGNOSIS. Macroconchs 150–195 mm. in diameter with following rib densities: at 20 mm. diameter there are 52–58 ribs; at 25, 55–60; 30, 56–63; 35, 60–65; 40, 62–67; 45, 65–71; 50, 68–74; 55, 70–76; 60, 73–77; 65, 75–79. Ribs of inner whorls slender and prorsiradiate. Outer whorl developing strengthened primary ribs, first with polygyrate and polyploke furcation, then with tendency to virgatotome furcation. Microconchs 77–110 mm. diameter with following rib densities: at 20 mm. diameter there are 47–50 ribs; at 25, 48–52; 30, 50–54; 35, 51–55; 40, 51–56. Ribs of inner whorls slender and prorsiradiate, becoming somewhat coarser on outer whorl with occasional polygyrate and simple ribs. Peristome with ventral horn 12–24 mm. long.

HOLOTYPE. Macroconch C.73437.

PARATYPE. Microconch C.73438.

MATERIAL. Twenty-eight specimens (fourteen macroconchs, thirteen microconchs, one intersex).

HORIZON. Both holotype and paratype from shales 13 ft. above the Rope Lake Head Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, lower part of Hudlestoni Zone, 12–16 ft. above the Rope Lake Head Stone Band.

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 150–195 mm. Diameter of the umbilicus 63–87 mm. The holotype is 157 mm. in diameter and has an umbilical diameter of 67 mm There are 64 primary and 141 secondary ribs on the last whorl. At 15 mm. diameter there are about 52 ribs; at 20, 58; 25, 60; 30, 63; 35, 63; 40, 65; 45, 65; 50, 68; 55, 70; 60, 74; 65, 75. The variation in rib density is shown in Text-fig. 7.

In style of ribbing on both inner and outer whorls this subspecies agrees closely with the description of *P.* (*V.*) *reisiformis* given above (p. 50). It differs, however, in being far more densely ribbed throughout. The ribs themselves are also a little more slender.

Microconch. Evolute shell with a diameter of 77–110 mm. Diameter of the umbilicus 27–42 mm. The paratype has a diameter of 83 mm. and an umbilical diameter of 30 mm. There are 67 primary and 132 secondary ribs on the last whorl. At 15 mm. the paratype has an estimated 46 ribs, at 20, 50; 25, 50; 30, 52. The variation is rib density is shown Text-fig. 7.

The rib style on the inner whorls is similar to that of the microconch of *P.* (*V.*) *reisiformis*, but the ribs are usually a little more prorsiradiate and are more slender.

On the outer whorl the ribs become a little coarser, and occasional polygyrate and simple ribs are developed.

The peristome margin may be straight or sinuous, a horn is developed ventrally, and on the paratype projects from the venter by 16 mm. In some cases growth has proceeded a little beyond the growth of the horn, and there is a fairly smooth zone anterior to this. In other cases a further horn may be grown close to the first one.

Intersex. This subspecies is particularly interesting because of a probable mutation which arose resulting in the development of inter-sexual individuals. One specimen (C.73439, Pl. 24, fig. 2) is intermediate in size between macroconch and microconch (117 mm. diameter) and has rib density of a typical microconch up to a diameter of 30 mm. (20, 47; 25, 49; 30, 52). Thereafter it becomes more finely ribbed (35, 56; 40, 58), and is intermediate between macroconch and microconch in rib density. (Text-fig. 7).

At a diameter of 94 mm. a horn is developed, and beyond this there is about three-eighths of a whorl of coarsely ribbed shell with sculpture similar to the outer whorls of a macroconch, but bearing four further horns. The development in this subspecies of the macroconch outer whorl sculpture at such a small diameter is unique to this specimen.

In addition to the above specimen which is absolutely intermediate in character between macroconch and microconch, three other specimens show a slight degree of intersexuality. These three specimens are apparently normal macroconchs to judge by their size, rib density and sculpture. They do, however, develop a type of horn in the later stages of development; this appears at a diameter of 140–150 mm. and is unlike the true microconch horn in that it is developed from a single rib, has negligible ventral projection but projects laterally some distance down the whorl side. In addition, the diameter at which these structures are developed is much greater than that at which the true horn of the microconch occurs.

These three latter specimens possess some degree of microconch character.

Remarks. This subspecies shows a general similarity to *P.* (*V.*) *reisiformis* described above. It may readily be distinguished, however, by the rib density of the inner whorls. Because of this likeness to *P.* (*V.*) *reisiformis*, the similar horizon of the two forms (this subspecies is confined to the beds yielding the youngest specimens of *P.* (*V.*) *reisiformis*) tends to confirm the view that it should be considered a direct derivative of *P.* (*V.*) *reisiformis.*

Pectinatites* (*Virgatosphinctoides*) *abbreviatus sp. nov.

(Pl. 26, fig. 3)

Diagnosis. Macroconchs small (113–125 mm. in diameter) with following rib densities: at 20 mm. diameter there are 40–42 ribs; at 25, 41–43; 30, 42–44; 35, 44–45; 40, 454–6; 45, 46. Ribs on inner whorls slender, rursiradiate to rectiradiate. Primary ribs becoming more widely spaced and stronger on outer whorl, with development of simple and polygyrate ribs. Microconchs unknown.

Holotype. Macroconch C.73440.

Material. Three specimens (all macroconchs).

Horizon. Holotype from shales 20 ft. above the Rope Lake Head Stone Band.

Stratigraphical range. Upper Kimmeridgian, Hudlestoni Zone (lower part), 20–22 ft. above the Rope Lake Head Stone Band.

Description. *Macroconch.* Evolute shell with a diameter of 113–125 mm. Diameter of umbilicus 45–59 mm. The holotype has a diameter of 113 mm. and an umbilical diameter of 45 mm. There are 47 primary and 96 secondary ribs on the last whorl. At 15 mm. diameter the holotype has 39 ribs; at 20, 40; 25, 41; 30, 42; 35, 44; 40, 45; 45, 46. The variation in rib density is shown in Text-fig. 6.

The ribs on the inner whorls are rursiradiate at the umbilical shoulder, they then bend forwards to become rectiradiate. Some of the ribs are, however, rursiradiate throughout their length. The point of bifurcation is high on the whorl-side. The umbilical seam uncoils over the last half whorl.

On the outer whorl, the ribs gradually become coarser, and on the last half whorl (which to judge by differences in the crushing corresponds to the length of the body-chamber) the primary ribs become widely spaced. Several simple, polygyrate and intercalatory ribs are developed.

The peristome is damaged on all the specimens, but on the holotype it is partially preserved and appears to be straight and simple.

The microconch of this species is unknown.

Remarks. This species is notable for the small size at which the macroconch becomes mature. For this reason it is unlikely to be confused with any other species of the genus. *P.* (*V.*) *wheatleyensis minor* is of similar size, but the outer whorl of this subspecies is ornamented by approximated mainly polygyrate ribs; this contrasts with the more widely spaced primary ribs of *P.* (*V.*) *abbreviatus*.

Pectinatites* (*Virgatosphinctoides*) *donovani sp. nov.

(Pl. 25, figs. 1, 2)

Diagnosis. Macroconchs 132–155 mm. in diameter with following rib densities: at 30 mm. diameter there are approximately 51 ribs; at 35, 51; 40, 51–53; 45, 51–54; 50, 52–55; 55, 53–55; 60, 55–56. Ribs on inner whorls slender and prorsiradiate. Outer whorl with strong irregular primary ribs with frequent polygyrate furcation. Simple and intercalatory secondary ribs abundant. Ribs fading slightly over last quarter of whorl. Microconchs 99–106 mm. in diameter with following approximate rib densities: at 30 mm. diameter there are 46 ribs; at 35, 48; 40, 49; 45, 50. Ribs of inner whorls similar to macroconch. Outer whorl developing somewhat stronger ribs with occasional simple and intercalatory ribs and polygyrate furcation.

Holotype. Macroconch C.73441.

Paratype (allotype). Microconch C.73442.

Material. Ten specimens, all plaster casts, (six macroconchs, four microconchs).

Horizon. Holotype from 30 ft. and paratype from 36 ft. below the Basalt Stone Band.

Stratigraphical range. Upper Kimmeridgian, Hudlestoni Zone (middle part), 30–40 ft. below the Basalt Stone Band.

Description. *Macroconch.* Evolute shell with a diameter of 132–155 mm. The diameter of the umbilicus varies from 59–69 mm. The holotype has a diameter of 137 mm. and an umbilical diameter of 65 mm. The last whorl of the holotype has 46 primary and 101 secondary ribs. At 40 mm. diameter the holotype has 52 ribs, at 45, 53; 50, 53; 55, 54; 60, 55; 65, 56. The variation in rib density is shown in Text-fig. 7.

The ribs on the inner whorl are rectiradiate at the umbilical shoulder, then curve forwards to become fairly straight and prorsiradiate. At the point of bifurcation, which is high on the whorl-side, the ribs curve back a little to the rectiradiate position. The umbilical seam uncoils over the last half to three-quarters of a whorl.

On the outer whorl the ribs gradually lose their initial rursiradial curve. The primary ribs become very strong and irregular, and the point of furcation is lower on the whorl-side. There are abundant simple, polygyrate and intercalatory ribs on the last whorl. Over the last quarter of a whorl, the ribs tend to fade somewhat, and although easily distinguishable, are not so prominent.

The peristome is somewhat sinuous and is simple.

Microconch. Evolute shell with a diameter of 99–106 mm. Diameter of the umbilicus 42–47 mm. The paratype has a diameter of 105 mm. and an umbilical diameter of 45 mm. The last whorl of the paratype has 49 primary and 96 secondary ribs. At 30 mm. diameter the paratype has 46 ribs, at 35, 48; 40, 49; 45, 50. The variation in rib density is shown in Text-fig. 7.

The ribs on the inner whorls are of similar style to those of the macroconch. The umbilical seam uncoils over the last half whorl (which appears to correspond to the length of the body-chamber, to judge by differences in the degree of crushing).

On the outer whorl the ribs become rather suddenly more widely spaced half a whorl from the aperture. These coarser ribs are rather irregular in their furcation; most are bifurcate, but there are several simple, polygyrate and intercalatory ribs.

The peristome is not completely preserved on any microconch of this species The dorsal part of it appears to be straight, but no specimen shows the whole of the ventral part which was presumably horned. The ventral part of the peristome of the paratype appears to project by some 5 mm., but is not well-preserved at this point.

Remarks. This species appears to be the one misidentified by Arkell as *P.* (*V.*) *wheatleyensis* (Arkell 1956 : 21). As I have shown earlier, however (p. 47), the true *P.* (*V.*) *wheatleyensis* occurs considerably lower in the succession, where it is associated with other species also characteristic of the Nodule Bed of Wheatley. The rib density and ornamentation of the body-chamber of *P.* (*V.*) *donovani* distinguish it from *P.* (*V.*) *wheatleyensis.*

Pectinatites* (*Virgatosphinctoides*) *magnimasculus sp. nov.

(Pl. 29)

Diagnosis. Microconchs very large (175–185 mm. in diameter) with following approximate rib densities: at 25 mm. there are 54 ribs; at 30, 55; 35, 57; 40, 57; 45, 59; 50, 60; 55, 62; 60, 62. Ribs of inner whorls slender, rectiradiate to slightly prorsiradiate. Outer whorl with similar style of ribs, remaining approximated but becoming a little coarser. Peristome with ventral horn 12–15 mm. long.

HOLOTYPE. Microconch C.73443.

MATERIAL. Two specimens, both plaster casts, microconchs.

HORIZON. Holotype from 21 ft. below the White Stone Band.

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Hudlestoni Zone (upper part), 18–21 ft. below the White Stone Band.

DESCRIPTION. Large evolute shell with a diameter of 175–185 mm. Diameter of umbilicus 77–82 mm. The number of primary ribs on the last whorl is estimated as about 70. The holotype which is 175 mm. in diameter and which has an umbilical diameter of 77 mm. has at a diameter of 25 mm. 54 ribs; at 30, 55; 35, 57; 40, 57; 45, 59; 50, 60; 55, 62; 60, 62. (Text-fig. 6). The other specimen's inner whorls are too poorly preserved to measure rib density.

The ribs on the inner whorls are fine and slender. They are rursiradiate at the umbilical shoulder, then curve forwards to become straight and rectiradiate, or slightly prorsiradiate. The point of bifurcation of the ribs is high on the whorl-side. The umbilical seam uncoils over the last half whorl.

The ribbing on the outer whorl is similar to that on the inner whorls. There is gradual coarsening of the ribs over the last whorl, but they are still approximated right up to the aperture.

The peristome is straight and bears a horn 15 mm. long on the holotype. Two other horns are also visible on the last whorl of the holotype. These are 11 and 13 mm. in length, and are ribbed. The other microconch specimen has three horns which in order of age are 6+; 19 and 12+ mm. in length.

REMARKS. Members of this species include the largest known horned microconchs. It is interesting to note that the ribs on the last whorl differ very little in style and density from those of the earlier whorls. It seems probable that several of the larger species of the subgenus *Virgatosphinctoides*, of which no microconchs have been found hitherto, have microconchs similar in size to those of *P.* (*V.*) *magnismasculus*.

Associated with the two microconch specimens was found a fragment of a large macroconch, which if complete would have had a diameter of about 320 mm. Its fragmentary nature and extremely poor preservation are such, however, that it cannot be referred to this species with any certainty.

Pectinatites* (*Virgatosphinctoides*) *encombensis sp. nov.

(Pl. 27, fig. 1; Pl. 28)

DIAGNOSIS. Microconchs 70–103 mm. in diameter with following rib densities: at 20 mm. diameter there are 42–43 ribs; at 25, 43–47; 30, 44–49; 35, 46–52. Ribs of inner whorls very slender, rectiradiate to slightly prorsiradiate. Ribs on outer whorl gradually becoming a little more widely spaced, with abundant polygyrate furcation on body-chamber. Peristome with ventral horn 9–15 mm. in length. Macroconchs 155–215 mm. in diameter with following very approximate rib densities:

at 55 mm. diameter there are 52 ribs; at 60, 54; 65, 56; 70, 57; 75, 58; 80, 59; 85, 60; 90, 61; 95, 63; 100, 64; 105, 65; 110, 66; 115, 67. Ribs of inner whorls similar to microconch. Outer whorl developing strengthened primary ribs becoming more widely spaced with occasional simple and polygyrate ribs and intercalatory secondaries.

Holotype. Microconch, C.73444.

Paratype (allotype). Macroconch C.73445.

Material. Ten specimens, all plaster casts (three macroconchs, seven microconchs).

Horizon. Holotype from 21 ft. and paratype from 33 ft. below the White Stone Band.

Stratigraphical range. Upper Kimmeridgian, Hudlestoni Zone (upper part), 9–33 ft. below the White Stone Band.

Description. The holotype is a microconch, since no really adequately preserved macroconchs have been discovered.

Microconch. Evolute shell with a diameter of 70–103 mm. Diameter of the umbilicus 28–38 mm. The holotype has a diameter of 103 mm. and an umbilical diameter of 38 mm. There are 63 primary and approximately 133 secondary ribs on the last whorl of the holotype.

At 20 mm. diameter there are 43 ribs, at 25, 47; 30, 48; 35, 49. The variation in rib density is shown in Text-fig. 6.

On the inner whorls the ribs are very slender. They are rursiradiate at the umbilical shoulder, then bend forwards to become fairly straight and rectiradiate or slightly prorsiradiate. The umbilical seam uncoils over the last half whorl.

The outer whorl is similarly ribbed, but gradually the ribs become a little more widely spaced and a little thicker. Abundant polygyrate ribs are developed on the last half whorl which appears to correspond to the length of the body-chamber.

The peristome is fairly straight and bears a ventral horn which varies in length from 11–20 mm. The holotype and two other specimens have additional horns a little way back from the peristome. The holotype has a total of three horns which (in order of age) are 15, 15 plus and 11 mm. long.

Macroconch. Evolute shell with a diameter of 155–215 mm. Diameter of umbilicus 75–118 mm. The paratype is the only macroconch showing any detail of the inner whorls. It is 215 mm. in diameter and has an umbilical diameter of 118 mm. There are approximately 68 primary and 122 secondary ribs on the last whorl. At 55 mm. diameter there are an estimated 52 ribs; at 60, est. 54; 65, est. 56; 70, est. 57 75, est. 58 80, est. 59. 85, est. 60; 90, est. 61; 95, est. 63; 100, est. 64; 105, est. 65; 110, est. 66; 115, est. 67. (Text-fig. 6).

The ribs on the inner whorls appear to be of a style similar to those of the microconch; on the last umbilical whorl they appear straight and rectiradiate throughout their length. On the last half whorl the primary ribs become more widely spaced and prominent, and their furcation becomes irregular. Several polygyrate, simple and intercalatory ribs are developed.

The peristome is simple.

REMARKS. Since the inner whorls are poorly preserved, the macroconch cannot be matched with the microconch as far as rib densities of the inner whorls go, but their association and similar sculpture strongly suggest that they are dimorphs of the same species.

This species is distinguished from others by its rib style and density. It bears some resemblance to *P.* (*V.*) *reisiformis* described above (p. 50) in rib density, but the ribs themselves are considerably more slender in *P.* (*V.*) *encombensis*. The macroconchs are not so variocostate as those of *P.* (*V.*) *reisiformis*, which provides another basis for distinction between these two species.

Subgenus ***PECTINATITES*** Buckman 1922

SYNONYMS. *Wheatleyites* Buckman 1923; *Keratinites* Buckman 1925; ? *Pectiniformites* Buckman 1925 (see p. 20).

TYPE SPECIES. (By original designation). *Ammonites pectinatus* Phillips 1871.

DIAGNOSIS. Dimorphic. Microconchs generally finely ribbed on inner whorls, body-chamber usually more coarsely ribbed. Peristome with ventral horn often of great length. Macroconchs generally finely ribbed on inner whorls. Outer whorls variable, primary ribs typically strong with variable number of secondary ribs. Never truly virgatotome. Both macroconch and microconch show tendency for ribs to bifurcate very low on whorl side. Constrictions generally absent.

Upper Kimmeridgian, ?Wheatleyensis Zone, Pectinatus Zone.

Ammonites pectinatus Phillips was the first species, now included in this genus, to be described. Phillips' figure (1871, pl. 15, fig. 17) is very poor, and the holotype has been long thought to have been lost. Arkell (1956 : 780) therefore designated a topotype as the neotype.

Pectinatites* (*Pectinatites*) *inconsuetus sp. nov.

(Pl. 30)

DIAGNOSIS. Macroconchs approximately 150 mm. in diameter. Ribs on outer whorl bifurcate low on whorl side. Ornamentation gradually fading on body-chamber. Peristome straight. Microconchs approximately 100 mm. in diameter. At 50 mm. diameter there are approximately 50 ribs. Point of bifurcation of ribs becoming gradually lower on whorl-side towards last whorl. Body-chamber more coarsely ribbed than inner whorls. Peristome bearing short ventral horn.

HOLOTYPE. Macroconch C.73446.

PARATYPE (ALLOTYPE). Microconch C.73447.

MATERIAL. Two specimens, both plaster casts (one macroconch, one microconch.

HORIZON. Both specimens from 10 ft. above the Middle White Stone Band. Upper Kimmeridgian, lower Pectinatus Zone.

DESCRIPTION. *Macroconch.* Evolute shell with a diameter of 153 mm. Diameter of umbilicus 65 mm. There are 26 primary and approximately 83 secondary ribs on the last whorl.

The ribs on the inner whorls are not well preserved, but are seen to be rursiradiate at the umbilical shoulder, then swinging forwards to become straight and slightly prorsiradiate. The primary ribs on the outer whorl at first become more pronounced and are more widely spaced. They branch very low on the whorl-side, giving rise to up to four secondary ribs. There are abundant intercalatory secondary ribs, which also arise very low on the whorl-side.

Over the last quarter of a whorl, the ribs gradually fade and become very indistinct.

The peristome which is straight and simple inclines anteriorly towards the venter.

Microconch. Evolute shell with a diameter of 98 mm. Diameter of the umbilicus 32 mm. There are 50 primary and an estimated 110 secondary ribs on the last whorl. There are approximately 50 ribs at a diameter of 30 mm.

The ribs on the inner whorls are fine and slender. They are rursiradiate at the umbilical shoulder, then curve forwards to become rectiradiate or slightly prorsiradiate. The point of bifurcation of the ribs is high on the whorl-side.

The umbilical seam uncoils over the last half whorl.

The ribs on the outer whorl are similar in style to those of the inner whorls, but gradually the point of bifurcation of the ribs becomes much lower on the whorl-side. Over the last half-whorl the primary ribs become stronger and more widely spaced, and usually give rise to three secondary ribs on the whorl-side. There are several simple and intercalatory ribs on the last half whorl.

The peristome bears a horn. On the paratype this is broken, and the resultant broken end has not reproduced well in the plaster. The basal 4 mm. of the horn are just visible, however.

REMARKS. I earlier referred the macroconch of this species to the Tithonian genus *Pseudovirgatites* (Cope & Zeiss 1964 : 12). At the time of making this identification, however, the microconch had not been discovered. The style of ribbing of the macroconch is very similar to some specimens of *Pseudovirgatites* from Franconia. However, the microconch, with its broadly similar ribbing on its body-chamber and horned peristome, shows that this species belongs to the genus *Pectinatites*.

This again is an example of the remarkable homeomorphy between the Tithonian and Upper Kimmeridgian ammonites which has misled so many workers in the past. This species of *Pectinatites* with its type of modification of the ribbing on the body-chamber of the macroconch is unlikely to be confused with any other species.

Pectinatites (Pectinatites) eastlecottensis (Salfeld)

(Pl. 26, fig. 1)

1913 *Perisphinctes eastlecottensis* Salfeld : 429, pls. 41, 42.
1914 *Perisphinctes eastlecottensis* Salfeld ; Salfeld : 130.
1922 *Wheatleyites eastlecottensis* (Salfeld) Buckman : 28.
1923 *Pectinatites aulacophorus* Buckman, pl. 381.
1925 *Wheatleyites eastlecottensis* (Salfeld) ; Neaverson : 37.
1933 *Pectinatites eastlecottensis* (Salfeld) Arkell : 457.

Material. Two specimens, plaster casts (both microconchs).

Horizon. Ten feet above the Middle White Stone Band. Upper Kimmeridgian, lower Pectinatus Zone.

Description. Neither of the two specimens from Kimmeridge is complete. The more complete of the two (C.73449, Pl. 26, fig. 1) has a diameter of 70 mm. and an umbilical diameter of approximately 22 mm. On the last half whorl preserved there are an estimated 58 primary and 97 secondary ribs. This would mean that at a diameter of 70 mm. there are about 100 ribs on a complete whorl.

The holotype, which is a macroconch, has 130 ribs at 110 mm. diameter. The holotype of *P. aulacophorus* Buckman has (according to Buckman) about 97 ribs at 66 mm. diameter.

The noticeable feature on the Dorset specimens is that the ribs often bifurcate very close to the umbilical shoulder.

The peristome is not preserved on either of the Dorset specimens but was probably originally horned.

Remarks. The extremely dense ribbing of this species is very characteristic. There can be little doubt that these Dorset specimens are the microconch of Salfeld's figured macroconch.

The holotype was quoted by Salfeld as coming from the Upper Lydite Bed at Swindon. Chatwin & Pringle (1921 : 166) later showed that in fact it came from the upper part of the Shotover Grit Sands. Buckman's species *P. aulacophorus* was quoted by him as occurring in his Bed 12 at Swindon—the bed which yielded the holotype of *P. eastlecottensis.*

Buckman's figure shows that the last sutures of *P. aulacophorus* are somewhat approximated, and that the umbilical seam is just beginning to uncoil. In this case it would appear that only the body-chamber is missing from this specimen, and it is, therefore, a microconch. Neaverson's figure (1925, pl. 1, fig. 5) of *P. aulacophorus* is an immature specimen of a species of the subgenus *Virgatosphinctoides* close to *P.* (*V.*) *wheatleyensis delicatulus.*

The occurrence of this species in Dorset enables good correlations to be made with Swindon and Oxford.

***Pectinatites* (*Pectinatites*) cf. *groenlandicus* (Spath)**

(Pl. 31)

1936 *Pectinatites* (*Keratinites?*) *groenlandicus* Spath : 25, pl. 6, fig. 1.

Material. One specimen (macroconch).

Horizon. Ten feet above the Middle White Stone Band. Upper Kimmeridgian, lower Pectinatus Zone.

Description. The single incomplete specimen from Kimmeridge has a crushed diameter of 380 mm. Diameter of umbilicus 177 mm. At 40 mm. diameter there are 48 ribs; at 50, 53; 60, 70, 80, 90, 51; 100, 52; 110, 120, 53; 130, 54; 140, 55; 150, 54; 160, 53; 170, 52.

There is a very close comparison between the Dorset specimen and the holotype which is from the Pectinatus Zone of Greenland. The furcation and style of the ribs on the inner whorls is very similar to that of the holotype (Spath, pl. 7, fig. 5). The point of bifurcation is very high on the whorl-side. The outer whorl is similar, too, with the ribs becoming less prominent towards the aperture of the shell. The peristome, which is not preserved, is presumably simple.

REMARKS. "*Wheatleyites*" *reductus* (Buckman) (1923, pl. 384) shows certain similarities to this species, but the inner whorls of this species are more sharply and densely ribbed.

Pectinatites* (*Pectinatites*) *cornutifer (Buckman)

(Pl. 25, fig. 3; Pl. 26, fig. 2)

1925 *Keratinites cornutifer* Buckman : pl. 602.
1926 *Keratinites nasutus* Buckman : pl. 664.

MATERIAL. Eight specimens (all microconchs).

STRATIGRAPHICAL RANGE. Upper Kimmeridgian, Pectinatus Zone (middle part), from 19 ft. below, to 6 ft. above the Freshwater Steps Stone Band.

DESCRIPTION. *Microconch.* Moderately evolute shell with a diameter of 68–90 mm. Diameter of the umbilicus 22–30 mm. There is good agreement with Buckman's figures in all respects. The horn is long and varies from 15 to 39 mm. in length. No macroconchs have been found at this horizon in Dorset (see below).

REMARKS. *K. cornutifer* Buckman is finer ribbed than *K. nasutus* Buckman. However, there is a complete transition in the Dorset specimens between these two forms. The *cornutifer* type occurs in the lower part, and the *nasutus* type in the upper part of the range of this species in Dorset. In the almost complete absence of macroconchs in collections from this horizon in Dorset, it is not possible to refer this species to one of the known macroconch species of *Pectinatites*. *P. pectinatus* (Phillips) occurs together with this species at Swindon and in the Oxford region, so that it may well be the macroconch of *P. cornutifer*.

Pectinatites* (*Pectinatites*) *naso (Buckman)

(Pl. 32)

1926 *Keratinites naso* Buckman, pl. 652.

MATERIAL. Three specimens, all plaster casts, (two macroconchs, one microconch).

HORIZON. Ten feet above the Freshwater Steps Stone Band. Upper Kimmeridgian, middle Pectinatus Zone.

DESCRIPTION. *Macroconch.* Fairly evolute shell with a diameter of 130–138 mm The diameter of the umbilicus is 50–54 mm. The figured specimen (C.73452) which has a diameter of 138 mm. and an umbilical diameter of 54 mm. has 40 primary ribs on the last whorl. At 25 mm. diameter there are about 45 ribs; at 30, 46; 35, 47; 40, 49; 45, 47; 50, 45.

The ribs on the inner whorls are rectiradiate at the umbilical shoulder, then curve forwards to become quite strongly prorsiradiate. The point of bifurcation of the ribs is high on the whorl-side.

On the outer whorl, just over half of which is preserved on the figured specimen, the primary ribs become stronger and more widely spaced. They branch fairly low on the whorl-side, giving rise to two or three secondary ribs. There are very occasional simple and intercalatory ribs.

The peristome is simple.

Microconch. The microconch (C .73453) is very similar to those figured by Buckman (pls. 652, 652*a*).

The Dorset specimen is 91 mm. in diameter, and has an umbilical diameter of 31 mm. There are an estimated 47 primary ribs on the last whorl. The preservation of the inner whorls is not good, and the following rib densities are only approximate: at 20 mm. 42 ribs; 25, 44; 30, 44.

The ribs on the inner whorls are similar in style to those of the macroconch. The umbilical seam uncoils over the last half whorl. On the outer whorl the ribs become rather suddenly more coarse half a whorl from the aperture. This last half whorl appears to correspond to the length of the body-chamber (to judge by differences in the degree of crushing). Buckman's specimens, too, have a body-chamber half a whorl in length.

On the last half whorl the primary ribs become more widely spaced; their point of furcation is lower on the whorl-side than on the inner whorls, and the angle of furcation increases. Most of the ribs on the body-chamber are bifurcate, but there are occasional unbranched primary ribs.

The peristome bears a horn which is 21 mm. long.

REMARKS. This species is readily distinguishable from *P. cornutifer* described above by the more coarsely ribbed body-chamber of the microconch.

The macroconch is considerably more coarsely ribbed than the macroconch of *P. pectinatus*.

Subfamily **DORSOPLANITINAE** Arkell 1950

Genus ***PAVLOVIA*** Ilovaisky 1917

Subgenus ***PARAVIRGATITES*** Buckman 1922

Pavlovia (Paravirgatites) cf. ***paravirgatus*** (Buckman)

(Pl. 33)

1922 *Paravirgatites paravirgatus* Buckman, pl. 353.

MATERIAL. One specimen C.73454.

HORIZON. Ten feet above the Freshwater Steps Stone Band. Upper Kimmeridgian, Pectinatus Zone (middle part).

DESCRIPTION. The single poorly preserved specimen has a diameter of 146 mm. and an umbilical diameter of 66 mm. There are 28 primary and an estimated 55 secondary ribs on the last whorl.

REMARKS. The specimen agrees closely with Buckman's figure in all respects except size. The holotype is about 220 mm. diameter. The general similarity and the similar horizon (Shotover Grit Sands) leave little doubt of the affinities of the Dorset specimen to Buckman's holotype.

V. EVOLUTION OF THE AMMONITES

The possible origin of the genus *Pectinatites* from an ataxioceratid stock has been discussed earlier (p. 22). Within the genus three subgenera are recognized and it is possible to follow in these subgenera various evolutionary trends.

The subgenus *Arkellites* first appears at the base of the Elegans Zone where it is represented by specimens referable to *P.* (*A.*) *primitivus*. *Arkellites* is characterized by more or less equicostate ribbing of the shell. This feature appears in the four species of the subgenus hitherto described. The macroconchs remain basically similar in rib style and ornamentation throughout the succession. In the microconchs, however, the tendency is for the horn to become much more prominent. *P.* (*A.*) *primitivus* has a weak ventral peristomal inflation, but all the later species have a well-developed true horn. The youngest species of *Arkellites* hitherto recorded, *P.* (*A.*) *hudlestoni*, shows a general similarity to these earlier species, and the conclusion is drawn that this subgenus was a fairly conservative one. There are as yet no species recorded from the Wheatleyensis Zone which can with certainty be placed in this subgenus, so that the connection between *P.* (*A.*) *hudlestoni* and earlier species of the subgenus is not known. However, *Paravirgatites kimmeridgensis* Neaverson (1925 : 33, pl. 4, fig. 4) has a rib density on its inner whorls close to that of *P.* (*A.*) *hudlestoni*, and may belong to this subgenus. The author cannot accept Neaverson's placing of his species in Buckman's genus *Paravirgatites*. The holotype shows the rib style, rib density and development typical of *Arkellites*, which is entirely different from the sharp regular bifurcate ribbing characteristic of the pavlovids. It is to be expected that the Wheatleyensis Zone will ultimately yield species which can definitely be assigned to the subgenus *Arkellites*.

The subgenus *Virgatosphinctoides* which appears in Dorset about a third of the way up the Elegans Zone could have been derived from *P.* (*A.*) *primitivus* (see p. 33). Unlike *Arkellites*, from which it probably arose, *Virgatosphinctoides* evolved rapidly. The horn of the microconch, represented by a ventral peristomal inflation in *P.* (*V.*) *elegans*, becomes a true horn by the top of the Elegans Zone (*P.* (*V.*) *elegans corniger*). Thereafter, the horn development becomes more pronounced, particularly in the Hudlestoni Zone. There are some species, however, (e.g. *P.* (*V.*) *woodwardi*) in which the horn development is not so pronounced. Considering next the macroconchs, the tendency seen is for the degree of variocostation of the shell to become more pronounced. Associated with this is the increase in the numbers of polygyrate ribs on the body-chamber. This trend continues with the appearance of virgatotome ribbing in the Wheatleyensis Zone. Some later forms from the Hudlestoni Zone (e.g. *P.* (*V.*) *donovani*) show, to some extent, a reversal of this trend, and the loss of the truly virgatotome rib type.

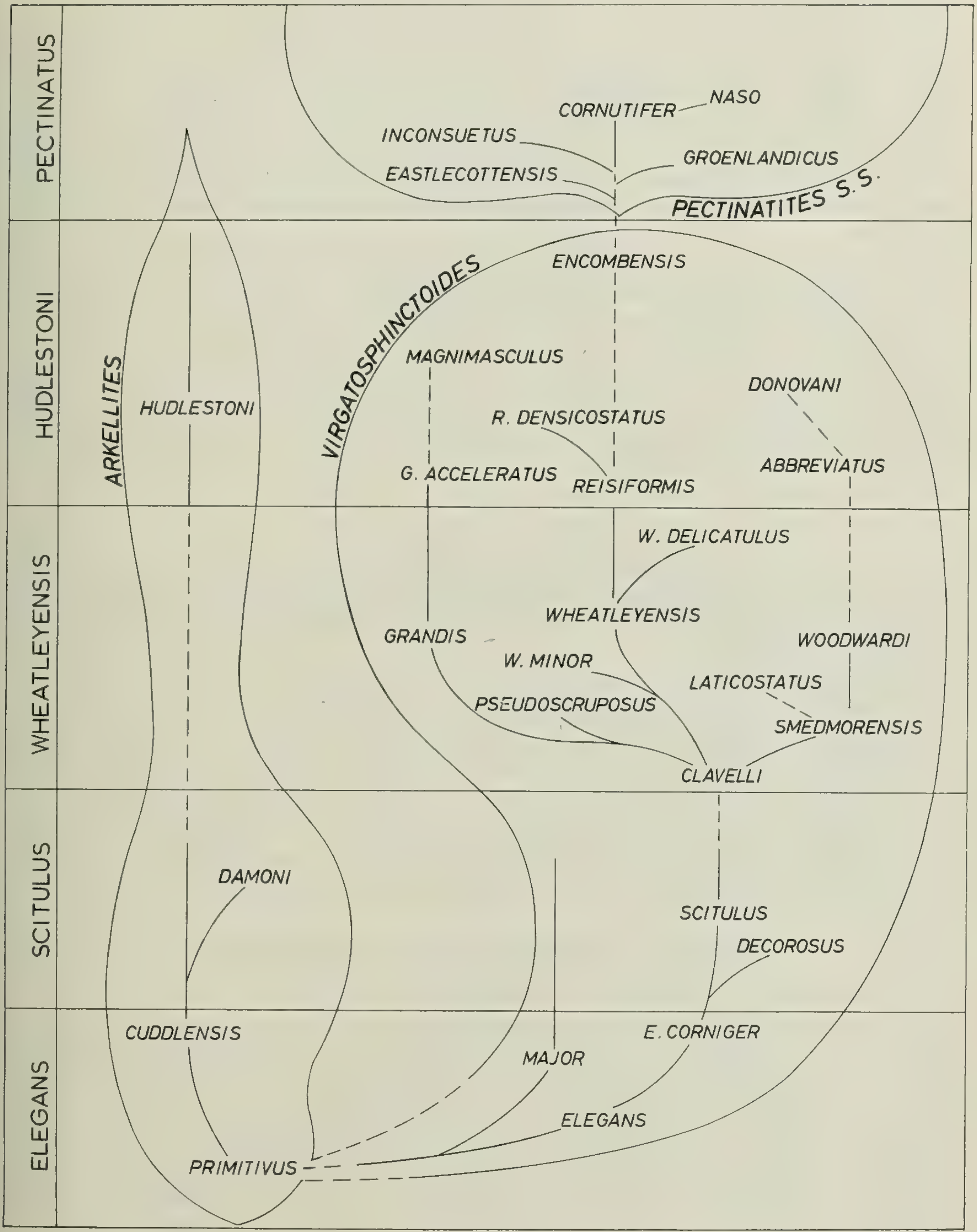

PECTINATUS
HUDLESTONI
WHEATLEYENSIS
SCITULUS
ELEGANS
NASO
CORNUTIFER
INCONSUETUS
GROENLANDICUS
EASTLECOTTENSIS
PECTINATITES S.S.
ENCOMBENSIS
VIRGATOSPHINCTOIDES
ARKELLITES
MAGNIMASCULUS
DONOVANI
HUDLESTONI
R. DENSICOSTATUS
G. ACCELERATUS
REISIFORMIS
ABBREVIATUS
W. DELICATULUS
WHEATLEYENSIS
GRANDIS
WOODWARDI
W. MINOR
LATICOSTATUS
PSEUDOSCRUPOSUS
SMEDMORENSIS
CLAVELLI
DAMONI
SCITULUS
DECOROSUS
CUDDLENSIS
E. CORNIGER
MAJOR
ELEGANS
PRIMITIVUS

FIG. 8. Possible phylogenetic relationships of species of *Pectinatites*.

The origins of the subgenus *Pectinatites* are almost certainly to be found in the subgenus *Virgatosphinctoides*. However, the actual point of origin is not clear. *Pectinatites* may be derived from such a form as *P.* (*V.*) *encombensis*, which has a finely ribbed shell, a microconch with a well-developed horn, and an absence of virgatotome ribs on the macroconch. Alternatively, the subgenus may have been derived from *Virgatosphinctoides* earlier, perhaps as early as the Wheatleyensis Zone. In *Pectinatites* the main trends observed, as far as the lower part of the Pectinatus Zone goes, appear to be the tendency for the ribs to bifurcate low on the whorl-side, and for the microconch horn to increase in length, reaching almost 40 mm. in *P.* (*P.*) *cornutifer*.

Homeomorphy occurs within the genus *Pectinatites*, particularly between species of the subgenera *Virgatosphinctoides* and *Pectinatites*. However, the homeomorphy always seems to appear in only one sex, and not in both sexes together.

Text-fig. 8 shows diagrammatically the possible relationships between the known species of the genus. It is not, of course, to be expected that this can represent an entirely complete picture. In particular, knowledge is scant at the base of the Elegans Zone, the upper part of the Scitulus Zone, and the lowermost Pectinatus Zone.

VI. THE AMMONITE ZONES

As a result of detailed collecting from the Kimmeridge section, the position of several species of ammonites, described from other areas, has been established for the first time. This has necessitated considerable modification of the existing table of zones (see Text-fig. 9).

Since the range of many species is known fairly accurately, it is proposed to set up a sub-zonal scheme, should this prove possible, at a future date. As a prerequisite for this, however, detailed knowledge of the ammonite faunas over a large area is considered necessary. Unfortunately the Oxford and Swindon areas, which could have yielded much from careful collecting, are now devoid of good, or even adequate, exposures of Upper Kimmeridge Clay. The sections in Yorkshire and Sutherland may, however, provide good information, particularly on the lower zones.

At this time, therefore, no further refinement than zonal subdivision is attempted.

Pectinatites* (*Virgatosphinctoides*) *elegans Zone

INDEX SPECIES. *Pectinatites* (*Virgatosphinctoides*) *elegans*.

This new zone is proposed for the beds between the thin cementstone band (Bed no. 42) and the Yellow Ledge Stone Band (Bed no. 36) of the Kimmeridge section.

This new zonal index replaces a zone based on species of the genus *Gravesia* which were first used for zonal subdivision of the Kimmeridge Clay by Salfeld. After his discovery in Dorset of species of ammonites, for which he proposed the genus, he set up two zones, for the shales between the Maple Ledge Stone Band (Arkell 1947 : 73) and the Yellow Ledge Stone Band, with species of *Gravesia* as their index fossils. He proposed an upper zone of *Gravesia irius* and a lower one of *Gravesia gravesiana* (Salfeld 1913).

PROPOSED ZONES	SALFELD 1913	NEAVERSON 1925	ARKELL 1956
PECTINATITES (PECTINATITES) PECTINATUS	*PERISPHINCTES PALLASIANUS*	*PECTINATITES PECTINATUS*	*PECTINATITES PECTINATUS*
PECTINATITES (ARKELLITES) HUDLESTONI	*VIRGATITES MIATSCHKOVENSIS*		*SUBPLANITES WHEATLEYENSIS*
PECTINATITES (VIRGATOSPHINCTOIDES) WHEATLEYENSIS		*VIRGATOSPHINCTOIDES NODIFERUS*	*SUBPLANITES GRANDIS*
PECTINATITES (VIRGATOSPHINCTOIDES) SCITULUS		*VIRGATOSPHINCTOIDES WHEATLEYENSIS*	*SUBPLANITES* SPP. ? *VIMINEUS*
PECTINATITES (VIRGATOSPHINCTOIDES) ELEGANS	*GRAVESIA IRIUS* *GRAVESIA GRAVESIANA*	*GRAVESIA* ZONES	*GRAVESIA GIGAS* *GRAVESIA GRAVESIANA*
AULACOSTEPHANUS ZONES			

FIG. 9. Zones of the lower part of the Upper Kimmeridge Clay.

Salfeld did not draw any junction between these two zones, and the specific identity of his specimens has long been in doubt. Arkell (1947 : 76) reported that he had seen Salfeld's specimens in Göttingen in 1937, but did not comment upon their identity. He called these two zones merely the *Gravesia* spp. zones (1947 : 67), and raised the lower limit of the zones in Dorset up to the unnamed cementstone band at the foot of Hen Cliff (about 65 ft. higher in the succession).

Later Arkell (1956 : 21) divided these Hen Cliff shales into an upper *Gravesia gigas* Zone and a lower *Gravesia gravesiana* Zone. Again, no boundary between these zones was fixed.

Arkell's raising of the upper limit of the *Aulacostephanus* Zones is justified by the occurrence of this genus up to about 15 ft. below the thin cementstone band referred to above. This band also marks the first appearance of specimens of *Pectinatites* (*Arkellites*), which are fragmentary and poorly preserved, but are probably close to *P.* (*A.*) *primitivus*.

The genus *Gravesia* is exceptionally rare in Dorset, and since 1913 only seven specimens of the genus have been found (three by Spath, two of which are in the British Museum, and one in the Geological Survey Museum; and four by the author). Of these ammonites, five are specimens of *Gravesia gigas* and have been found between 40 and 52 ft. below the Yellow Ledge Stone Band. The other two are referred to *Gravesia gravesiana* and came from eight feet below and six feet above the Yellow Ledge Stone Band (i.e. higher than any previously recorded specimens). No known *Gravesia irius* has been found since Salfeld's report of its abundant occurrence in 1913.

Whether or not *Gravesia irius* does in fact occur at Kimmeridge, it is clear that *Gravesia gravesiana* is restricted to beds higher than those yielding *Gravesia gigas*

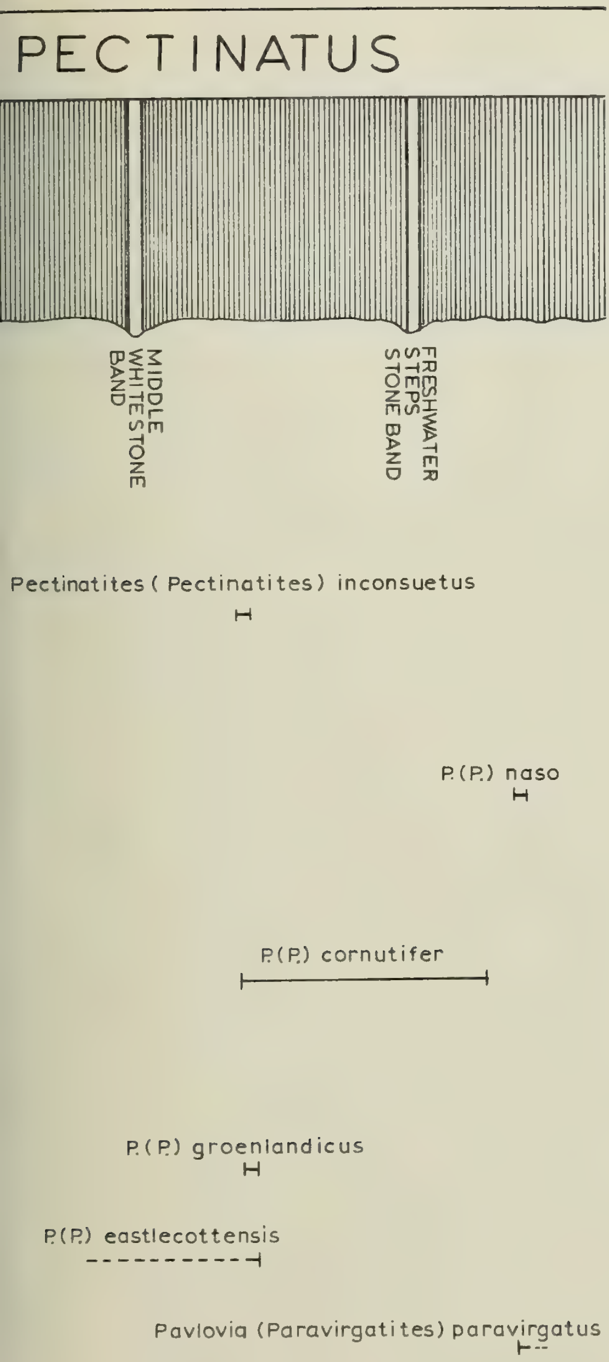
It is thus proposed to set up this zone based on a species of *Pectinatites*, since species of this genus are common in these beds in Dorset. This obviates any difficulty over fixing of boundaries of zones based on extremely rare index fossils, and since species of *Pectinatites* occur in this zone in Yorkshire (whereas *Gravesia* does not) there should in future be no ambiguity as in the past.

The base of the zone is fixed above the highest occurrence of *Aulacostephanus*, and at the earliest occurrence of *Pectinatites*. *P.* (*Arkellites*) *primitivus* occurs from the base of the zone into the upper part. *P.* (*V.*) *elegans* appears below the middle of the zone and ranges into the upper part, where it is replaced by *P.* (*V.*) *elegans corniger*. *P.* (*Arkellites*) *cuddlensis* occurs in the top 18 ft. of the zone. The top of the zone corresponds to the highest occurrence of *P.* (*V.*) *elegans corniger*. *Gravesia gigas* occurs just below the middle of the zone, *G. gravesiana* ranges from the highest part of the zone into the base of the succeeding Scitulus Zone.

***Pectinatites* (*Virgatosphinctoides*) *scitulus* Zone**

INDEX SPECIES. *Pectinatites* (*Virgatosphinctoides*) *scitulus* sp. nov.

This new zone is proposed for the shales between the Yellow Ledge Stone Band and the Grey Ledge Stone Band in the Dorset succession. This thickness of 90 ft. includes the Lower Cattle Ledge Shales (up to Cattle Ledge), and the Upper Cattle Ledge Shales (between Cattle Ledge and Grey Ledge).


PECTINATUS
MIDDLE WHITE STONE BAND
FRESHWATER STEPS STONE BAND
Pectinatites (Pectinatites) inconsuetus
P. (P.) naso
P. (P.) cornutifer
P. (P.) groenlandicus
P. (P.) eastlecottensis
Pavlovia (Paravirgatites) paravirgatus

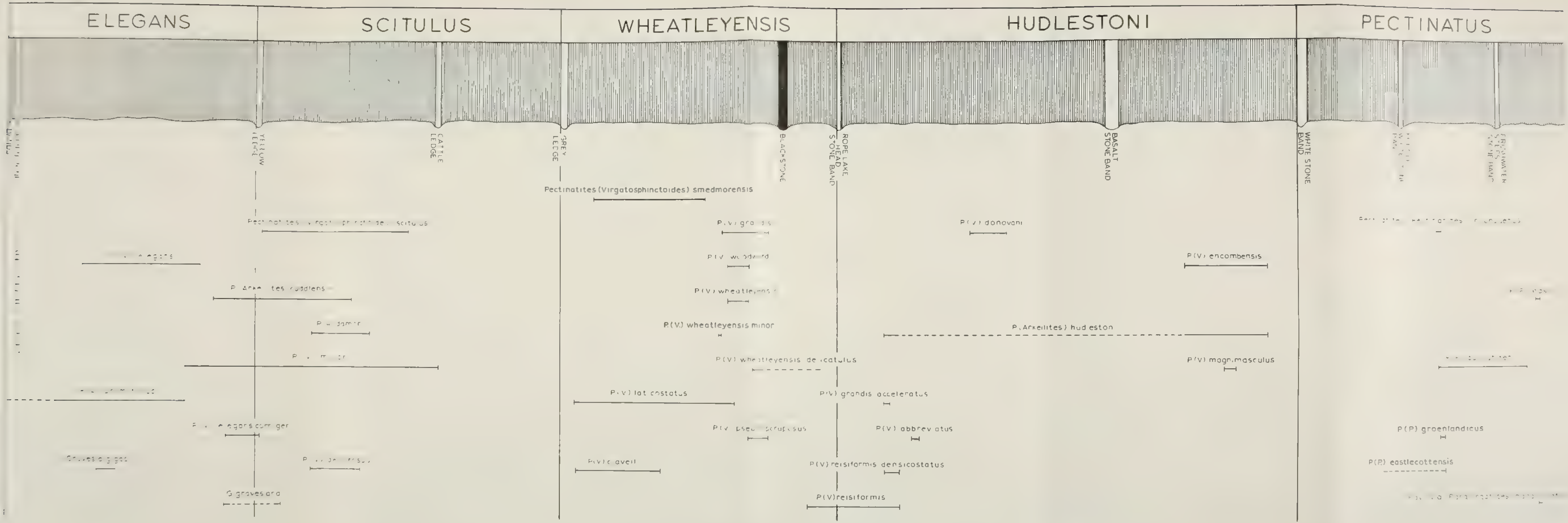


FIG. 10. Stratigraphical ranges of the ammonites from the lower part of the Upper Kimmeridge Clay

The Upper Cattle Ledge Shales have hitherto failed to yield ammonites and are provisionally included in this zone, pending ammonite evidence from Dorset or elsewhere.

Pectinatites (*Virgatosphinctoides*) *scitulus* first appears at the base of the zone, and ranges to about the middle of the ammonite bearing strata. *Gravesia gravesiana* occurs in the lowest six feet of the zone at Kimmeridge. *Exogyra virgula* ranges up to 27 ft. above the Yellow Ledge Stone Band. *Lingula ovalis* reaches its maximum abundance near the base of the zone.

This zone corresponds to the lower part of Salfeld's *Virgatites miatschkovensis* Zone, the lower part of Neaverson's *Virgatosphinctoides wheatleyensis* Zone, and the *Subplanites* ? *vimineus* Zone of Spath (Arkell 1956 : 21).

Pectinatites* (*Virgatosphinctoides*) *wheatleyensis Zone

Index species. *Pectinatites* (*Virgatosphinctoides*) *wheatleyensis* (Neaverson).

This zone, which in the Dorset succession is represented by the beds between the Grey Ledge Stone Band and the Rope Lake Head Stone Band, corresponds to part of the *Virgatites miatschkovensis* Zone of Salfeld (1913); the *Pseudovirgatites* Zone of Lamplugh, Kitchin & Pringle (1922); the lower part of the Pectinatus, the Nodiferus and the upper part of the Wheatleyensis Zone of Neaverson (1925); and to all but the uppermost part of the Grandis Zone of Arkell (1956).

The position of *Pectinatites* (*Virgatosphinctoides*) *wheatleyensis* (Neaverson) has hitherto been very uncertain in the Dorset succession. In Oxfordshire, it occurs associated with *P.* (*V.*) *woodwardi*, *P.* (*V.*) *wheatleyensis delicatulus* and *Sphinctoceras*. The same faunal association (without *Sphinctoceras*), but with *P.* (*V.*) *grandis* and *P.* (*V.*) *pseudoscruposus* in addition, is found in Dorset in the shales immediately below the Blackstone.

At the base of the zone ammonites of the subgenus *Virgatosphinctoides* are represented by *P.* (*V.*) *clavelli*, *P.* (*V.*) *smedmorensis* and *P.* (*V.*) *laticostatus*; the latter two species ranging up to the middle of the zone.

The crinoid *Saccocoma* ranges in Dorset through 13 ft. of Beds in the upper part of the Zone.

The top of the Zone corresponds to the highest occurrence of *P.* (*V.*) *wheatleyensis delicatulus* and the earliest occurrence of *P.* (*V.*) *reisiformis*.

The zone is represented in the Oxford district by the Wheatley Nodule Bed, and is present on the Yorkshire coast.

Pectinatites* (*Arkellites*) *hudlestoni Zone

Index species: *Pectinatites* (*Arkellites*) *hudlestoni* sp. nov.

This new zone is proposed for the beds between the Rope Lake Head Stone Band and the White Band in the Kimmeridge succession. It corresponds to the upper part of Salfeld's *Virgatites miatschkovensis* Zone, part of Neaverson's Pectinatus Zone, and to the Wheatleyensis Zone and topmost part of the Grandis Zone of Arkell. At the base of the zone *Pectinatites* (*Virgatosphinctoides*) *reisiformis* occurs, and a little above the base is associated with *P.* (*A.*) *hudlestoni* which ranges throughout the zone. The middle part of the zone is characterized by *P.* (*V.*) *donovani* and the upper part by *P.* (*A.*) *hudlestoni*, *P.* (*V.*) *encombensis* and *P.* (*V.*) *magnimasculus*.

Inland this zone may be represented by the Shotover Fine Sands and the Lower Cemetery Beds in the Oxford and Swindon areas respectively. There is no palaeontological evidence to support this correlation directly, however, and the zone, if present is certainly very much attenuated. It is probably present in Yorkshire.

Pectinatites (*Pectinatites*) *pectinatus* Zone

INDEX SPECIES. *Pectinatites* (*Pectinatites*) *pectinatus* (Phillips).

This zone corresponds to the *Perisphinctes pallasianus* Zone of Salfeld, the upper part of the Pectinatus Zone of Neaverson, and the Pectinatus Zone of Arkell.

In Dorset the lower boundary of the zone is taken at the White Stone Band which marks the upper limit of the range of the subgenus *Virgatosphinctoides*, and the upper boundary below the first occurrence of *Pavlovia* s.s. The upper part of this zone has not yet been fully investigated in Dorset.

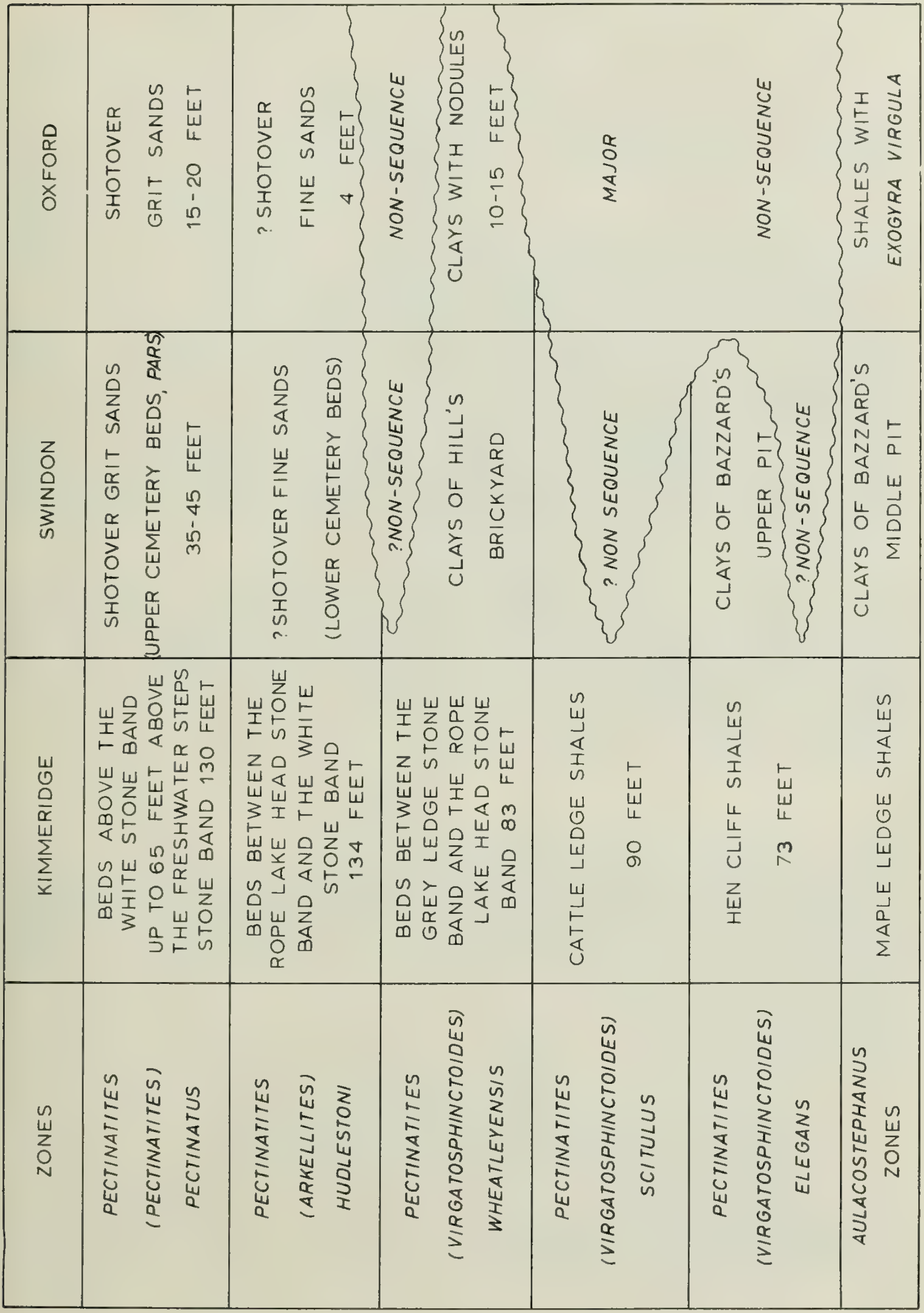
The earliest species recorded in Dorset is *Pectinatites* (*Pectinatites*) *eastlecottensis*; this species is recorded together with such species as *P.* (*P.*) *cornutifer* and *P.* (*P.*) *naso* from the Shotover Grit Sands in the Oxford region. No detailed stratigraphical collections have been made from these beds in the Oxford region, however, and it may be that they are not in fact completely synchronous, as published faunal lists suggest. In Dorset there is little overlap of the ranges of these species (Text-fig. 10), and it is to be expected that detailed collecting would show similar relationships between the various ranges of species in the Oxford area, where the succession is considerably thinner.

VIII. CORRELATIONS

(a) GREAT BRITAIN

The Upper Kimmeridge Clay is exposed in only a limited number of localities in Britain, and of these few exposures most are now very poor. The majority of the published faunal lists from these exposures are now outdated, and nowhere have collections been made in detail comparable to that recently carried out in Dorset. For these reasons, correlations with other areas of Britain cannot, in most cases, be established with a great deal of accuracy at present. It is hoped that future collecting will remedy this deficiency.

Two areas of Britain where the succession of the Kimmeridgian faunas have been well known for some time are the Swindon and Oxford regions. Correlations with these areas are shown in Text-fig. 11. In both these areas the succession is considerably attenuated. The ammonites, however, are generally better preserved than those in Dorset and have therefore attracted considerably more attention in the past. It was primarily on information obtained from the Oxford area that Neaverson (1925) set up his zonal scheme for the Upper Kimmeridge Clay. It is now possible for the first time to show the true stratigraphical position of many of Neaverson's species in the complete Dorset succession. As a direct result of this, it appears likely that there



ZONES	KIMMERIDGE	SWINDON	OXFORD
PECTINATITES (PECTINATITES) PECTINATUS	BEDS ABOVE THE WHITE STONE BAND UP TO 65 FEET ABOVE THE FRESHWATER STEPS STONE BAND 130 FEET	SHOTOVER GRIT SANDS UPPER CEMETERY BEDS, *PARS* 35-45 FEET	SHOTOVER GRIT SANDS 15-20 FEET
PECTINATITES (ARKELLITES) HUDLESTONI	BEDS BETWEEN THE ROPE LAKE HEAD STONE BAND AND THE WHITE STONE BAND 134 FEET	? SHOTOVER FINE SANDS (LOWER CEMETERY BEDS)	? SHOTOVER FINE SANDS 4 FEET *NON-SEQUENCE*
PECTINATITES (VIRGATOSPHINCTOIDES) WHEATLEYENSIS	BEDS BETWEEN THE GREY LEDGE STONE BAND AND THE ROPE LAKE HEAD STONE BAND 83 FEET	*?NON-SEQUENCE* CLAYS OF HILL'S BRICKYARD	CLAYS WITH NODULES 10-15 FEET
PECTINATITES (VIRGATOSPHINCTOIDES) SCITULUS	CATTLE LEDGE SHALES 90 FEET	*? NON SEQUENCE*	*MAJOR*
PECTINATITES (VIRGATOSPHINCTOIDES) ELEGANS	HEN CLIFF SHALES 73 FEET	CLAYS OF BAZZARD'S UPPER PIT *? NON-SEQUENCE*	*NON-SEQUENCE*
AULACOSTEPHANUS ZONES	MAPLE LEDGE SHALES	CLAYS OF BAZZARD'S MIDDLE PIT	SHALES WITH *EXOGYRA VIRGULA*

FIG. 11. Correlation of the lower part of the Upper Kimmeridge Clay of Kimmeridge with that of the Swindon and Oxford areas.

is a previously undetected non-sequence in both the Oxford and Swindon areas, between the Pectinatus and Wheatleyensis Zones, corresponding to the Hudlestoni Zone. This zone may be represented in part, however, by the Shotover Fine Sands.

Between the Lower and Upper Kimmeridge Clay there is a major non-sequence in the Oxford area. Above the *Aulacostephanus* Zones are beds yielding *Pectinatites* (*Virgatosphinctoides*) *wheatleyensis*. There are no known records of fossils indicative of the Elegans or Scitulus Zones. At Swindon, however, the position is different. Chatwin & Pringle (1922 : 165) mention that the Hudleston collection contains a specimen of *Gravesia* from Swindon, and it is therefore possible that the succession in this region, though attenuated, is fairly complete.

In Yorkshire the Kimmeridge Clay is exposed beneath the Lower Cretaceous rocks which rest unconformably on it at Speeton. The Kimmeridge Clay here is little known palaeontologically. The highest horizon recorded in this section is the Wheatleyensis Zone, but a specimen sent to me by Dr. P. Kaye from the highest beds of the Kimmeridge Clay, is undoubtedly close to *Pectinatites* (*P.*) *proboscide* (Buckman), requiring correlation with the Pectinatus Zone. There appears no reason to believe that the Yorkshire succession is not complete up to this latter zone. The Elegans Zone in Yorkshire is unlikely to yield *Gravesia* since the presence of this genus has not been confirmed north of Swindon.

In Sutherland, the lowest part of the Upper Kimmeridge Clay appears to be present, to judge from the account by Bailey & Weir (1932). Above the *Aulacostephanus* zones they recorded species of *Lithacoceras* indicative of the *Gravesia* zones, and evidence for the lower part of the *Virgatites* zone. I interpret this evidence as showing that the Elegans and possibly Scitulus Zones are present. The record of *Lithacoceras* presumably refers to a species of *Pectinatites* perhaps of the Elegans Zone. This area is one from which collecting is planned in the future.

(b) THE BOULONNAIS

The Upper Kimmeridgian of the Boulonnais shows similarities to the Kimmeridgian of Britain. It is remarkable chiefly for the development of phosphatic nodule beds at several horizons. The succession below is based on descriptions by Pruvost (1924), with modifications after Arkell (1956 : 42) and revised determinations of the ammonite names.

Bed. No. (Pruvost) 1924)

Ph. 3. Tour Croi Nodule Bed with phosphatized ammonites: *Pavlovia rotunda*, *P. leblondi*, *Pectinatites* (*Pectinatites*) *devillei*, *P.* (*P.*) *boidini*, *Pectinatites* (*P.*) *rarescens*, *P.* (*P.*) *opulentus*.

5. Clay 26 ft.: *P.* (*P.*) *devillei*, *P.* (*P.*) *boidini*, *P.* (*P.*) sp., *Pavlovia lydianites*, *Exogyra dubiensis*.

Ph. 2. Phosphatic nodule Beds: undescribed ammonites:

4. Clay 6 ft. 6 ins.: undescribed ammonites, *Lingula ovalis*, *Discina latissima*, *Modiola autissiodorensis*, *Anomia laevigata*.

Ph. 1. La Rochette Nodule bed: *Pectinatites* (*Virgatosphinctoides*) *pringlei*, *P.* (*V.*) spp.
3. Clays 26 ft. *Discina latissima*, *Pectinatites* (*Virgatosphinctoides*) spp.
2. Gres de la Creche (upper part) 16 ft.: *Pectinatites* (*Virgatosphinctoides*) sp.
1. Gres de la Creche (lower part) 32 ft. 6 ins. *Gravesia portlandica* (? =*G. gigas*), " *Perisphinctes* " *bleicheri*, *Trigonia pellati*, *Exogyra virgula*.

Aulacostephanus Zones.

Again the ammonite fauna of these beds is not well known, but on the basis of the recorded species and the associated fauna, several correlations may be suggested.

Bed 1 corresponds to the Elegans Zone. *Gravesia portlandica* (de Loriol) is probably a junior synonym of *G. gigas* (*Zieten*). *Trigonia pellati* and *Exogyra virgula* also occur in this zone in Dorset.

Beds 2–4 probably correspond to the Scitulus, Wheatleyensis and Hudlestoni Zones. *Pectinatites* (*Virgatosphinctoides*) *pringlei* (horizon Ph. 1) is close to *P.* (*V.*) *wheatleyensis*, and is probably, therefore, from the mid-Wheatleyensis Zone.

Bed 5 appears to correspond to the upper part of the Pectinatus Zone, and the Tour Croi Nodule Bed to the Rotundum Zone.

(c) East Greenland (Milne Land)

The Kimmeridgian fauna of Greenland were the subject of papers by Spath (1935, 1936). He described therein collections made on expeditions led by Dr. Lauge Koch.

The Upper Kimmeridgian succession there (Spath 1936 : 163) is:

Pavlovia Beds. 150 ft.
Pectinatites Beds. 150 ft.
Unfossiliferous Shales. 120 ft.
Band of crushed Perisphinctids.

The *Pectinatites* Beds correspond to the Pectinatus Zone of Dorset. Specific identity is established with Dorset in two cases.

The band of crushed Perisphinctids yielded three specimens which Spath identified tentatively as *Subdichotomoceras?*, *Subplanites?* (*Virgatosphinctoides?*), and *Subplanites?* (Spath 1936, pl. 1). The latter two specimens appear from the plate to resemble forms from the Wheatleyensis Zone, and are probably to be correlated with this zone. The unfossiliferous beds between these two points of correlation probably representing the Hudlestoni Zone of Dorset. No fauna to be correlated with Elegans or Scitulus Zones is recorded from East Greenland.

(d) Southern Germany (Franconia)

In the southern part of Europe the ammonite fauna of the Upper Jurassic rocks becomes markedly different from that of North-west Europe, above the Lower Kimmeridgian. To these rocks equivalent to the Upper Kimmeridgian and Portlandian Stages of North-west Europe the stage name " Tithonian " is generally applied.

SUGGESTED CORRELATIONS (MODIFIED AFTER COPE AND ZEISS 1964)		CORRELATIONS BY ARKELL 1956	
GLAUCOLITHITES GOREI	NEUBERG BEDS	CORRELATIONS BETWEEN THE UPPER KIMMERIDGIAN AND LOWER PORTLANDIAN OF BRITAIN AND THE LOWER TITHONIAN OF GERMANY	
ZARAISKITES ALBANI			
PAVLOVIA PALLASIOIDES			
PAVLOVIA ROTUNDA			
PECTINATITES (PECTINATITES) PECTINATUS	RENNERTSHOFEN BEDS	NEUBERG BEDS	*PECTINATUS ?*
PECTINATITES (ARKELLITES) HUDLESTONI		RENNERTSHOFEN BEDS	*SUBPLANITES* SPP.
PECTINATITES (VIRGATOSPHINCTOIDES) WHEATLEYENSIS	USSELTAL BEDS		
PECTINATITES (VIRGATOSPHINCTOIDES) SCITULUS	MOERNSHEIM BEDS	UPPER ULMENSIS BEDS	?
PECTINATITES (VIRGATOSPHINCTOIDES) ELEGANS		SOLENHOFEN BEDS	*GIGAS* *GRAVESIANA*

FIG. 12. Correlations between the Upper Kimmeridgian and Lower Portlandian of Britain, and the Lower Tithonian of Franconia.

The area taken herein, as representative of typical Tithonian rocks, is Franconia. I have recently visited this area, and have examined large ammonite collections made by Dr. A. Zeiss of the University of Erlangen, with whom I discussed problems of correlation between the two faunal provinces. The results of these discussions were incorporated in a joint paper (Cope & Zeiss 1964).

The most firm bases for correlation are to be found between the basal and uppermost Upper Kimmeridgian and basal Portlandian, and their Franconian equivalents. In the Lower Neuberg Beds specimens of *Pavlovia* and *Zaraiskites* have recently been found. This gives good correlations with the uppermost Kimmeridgian and basal Portlandian of Dorset. The discoveries are particularly important since it means that the Kimmeridgian–Portlandian boundary can be traced into the Tithonian faunal province.

At the base of the Upper Kimmeridgian the genus *Gravesia* occurs, its vertical range in Dorset being about 60 ft. In Franconia, *Gravesia* occurs in the Moernsheim Beds where its vertical range is about 90 ft.

Between these two points where correlation can definitely be established, the faunas of the two provinces are distinct. In Britain species of *Pectinatites* are the commonest ammonites, and in Franconia species of *Subplanites*, *Lithacoceras* and *Pseudovirgatites*. As stated earlier (p. 20) *Subplanites* and *Lithacoceras* do not occur in Britain. It therefore appears that the apparent similarity between the two faunas is due entirely to the phenomenon of homeomorphy.

It is remarkable to find that some homeomorphs seem to have existed contemporaneously. Thus some ammonites of the *Pectinatites* (*Virgatosphinctoides*) *grandis* group are very close to undescribed ammonites from the Usseltal Beds. *P.* (*Virgatosphinctoides*) *reisiformis* has a very similar microconch to *Subplanites siliceus*, the apertural modifications of the two forms being the only apparent point of difference. *P.* (*Pectinatites*) *inconsuetus* has a macroconch almost identical in appearance to an undescribed species of *Pseudovirgatites*.

Such homeomorphs cannot provide correlations, but it has been found that their respective stratigraphical ranges are approximately equal in some cases. It appears that direct correlation by means of ammonites is not possible in this case, and the problem is unlikely to be solved until an area is discovered where an overlap of the faunal provinces occurs.

(e) Russia (Basin of the Ural and Ilek Rivers)

The Upper Kimmeridgian faunas of the basin of the Ural and Ilek rivers were described by Ilovaisky & Florensky (1941). The specimens they described came from the Vetlianka Sandstone, and were described as belonging to the genus *Ilovaiskya* Vialov 1940. This genus was regarded by Arkell (1957) as a junior synonym of *Subplanites* Spath 1925.

Although several of the forms figured by Ilovaisky & Florensky appear very similar to British species, and were identified as such by Arkell (1956 : 489–490), identity even at generic level with British forms cannot be established on the basis of the published plates. None of the ammonites figured by Ilovaisky & Florensky has its peristome preserved, and thus may belong equally to *Subplanites* or its homeomorph *Pectinatites*. As no specimens similar to *Lithacoceras* were figured, it is possible that the Russian forms belong to *Pectinatites* rather than to *Subplanites*. The collection of material with peristomes intact is essential, however, for this to be established with certainty.

This problem has not been resolved in a more recent paper by Michailov (1964). He figures specimens under the names of *Subplanites* and *Pectinatites*. It may well be that in parts of Russia there is a mixture of these two faunal elements, but again the absence of peristome-bearing specimens means that such generic placings by Michailov may be incorrect.

VIII. REFERENCES

ARKELL, W. J. 1933. *The Jurassic System in Great Britain.* xii + 681 pp., 41 pls., 97 figs. Oxford.

—— 1935. On the Lower Kimmeridgian ammonite genera *Pictonia, Rasenia, Aulacostephanus* and *Ataxioceras*. *Geol. Mag.*, London, **72** : 246–257, pl. 11.

—— 1935–1948. A monograph of the ammonites of the English Corallian Beds. lxxxiv + 420 pp., 78 pls. *Palaeontogr. Soc.* (*Monogr.*), London.

—— 1946. Standard of the European Jurassic. *Bull. geol. Soc. Am.*, New York, **57** : 1–34.

—— 1947. *The geology of the country around Weymouth, Swanage, Corfe, and Lulworth.* xii + 386 pp., 19 pls. (Mem. geol. Surv. U.K., London).

—— 1947*a*. *The geology of Oxford.* vi + 267 pp., 6 pls. Oxford.

—— 1950. A classification of the Jurassic ammonites. *J. Paleont.*, Tulsa, **24** : 354–364.

—— 1953. Seven new genera of Jurassic ammonites. *Geol. Mag.*, London, **90** : 36–40, pl. 1.

—— 1956. *Jurassic Geology of the World.* xv + 806 pp., 46 pls. Edinburgh & London.

ARKELL, W. J., KUMMEL, B. & WRIGHT, C. W. 1957. Mesozoic Ammonoidea. In *Treatise on Invertebrate Paleontology*. Part L. Mollusca 4. Cephalopoda, Ammonoidea. (Ed. by R. C. Moore). L80–L437. Kansas & New York.

BAILEY, E. B. & WEIR, J. 1932. Submarine faulting in Kimmeridgian times in East Sutherland. *Trans. R. Soc. Edin.*, **57** : 429–467, pls. 1–3.

BASSE, E. 1930. Contribution à l'étude du Jurassique supérieur (facies corallien) en Ethiopie et en Arabie méridionale. *Mém. Soc. géol. Fr.*, Paris (n.s.) **6** : 105–148, pls. 4, 5.

—— 1952. Céphalopodes. *In* Piveteau, J. 1952. *Traité de Paléontologie*, **2** : 461–755, pls. 1–24. Paris.

BERCKHEMER, F. & HÖLDER, H. 1959. Ammoniten aus dem Oberen Weissen Jura Süddeutschlands. *Beih. geol. Jb.*, Hannover, **35** : 1–135, 27 pls.

BLAKE, J. F. 1875. On the Kimmeridge Clay of England. *Q. Jl geol. Soc. Lond.*, **31** : 196–237.

—— 1880. On the Portland rocks of England. *Q. Jl geol. Soc. Lond.*, **36** : 189–236.

—— 1881. On the correlation of the Upper Jurassic rocks of England with those of the Continent. Part 1. The Paris Basin. *Q. Jl geol. Soc. Lond.*, **37** : 497–587.

BLANCHET, F. 1923. La faune du Tithonique inférieur des régions subalpines et ses rapports avec celle du Jura franconien. *Bull. Soc. géol. Fr.*, Paris (4) **23** : 70–80.

BUCKMAN, S. S. 1922–1923. *Type Ammonites*, **4** : 1–67, pls. 268A–422. London.

—— 1923–1925. *Type Ammonites*, **5** : 1–88, pls. 423–576. London.

—— 1925–1927. *Type Ammonites*, **6** : 1–61, pls. 528A–717B. London.

—— 1927–1930. *Type Ammonites*, **7** : 1–78, pls. 31A–773A. With editorial notes by A. Morley Davies. London & Thame.

BUCKMAN, S. S. & BATHER, F. A. 1894. Can the sexes in ammonites be distinguished? *Nat. Sci.*, London, **4** : 427–432.

Callomon, J. H. 1955. The ammonite succession the Lower Oxford Clay and Kellaways Beds at Kirtlington, Oxfordshire, and the zones of the Callovian Stage. *Phil. Trans. R. Soc.*, London, **239**, B : 215–264, pls. 2, 3.

—— 1957. Field meeting in the Oxford Clay of Calvert and Woodham Brick Pits, Buckinghamshire. *Proc. Geol. Ass.*, London, **68** : 61–64.

—— 1961. The Jurassic System in East Greenland. *In* Raasch, G. O. 1961 (Editor). *Geology of the Arctic* : 258–268. Toronto.

—— 1963. Sexual dimorphism in Jurassic ammonites. *Trans. Leicester lit. phil. Soc.*, **57** : 21–56, pl. 1.

Chatwin, C. P. & Pringle, J. 1922. The zones of the Kimmeridge and Portland rocks at Swindon. *Summ. Progr. Geol. Surv. Lond.*, **1921** : 162–168.

Cope, J. C. W., Sarjeant, W. A. S., Spalding, D. A. E. & Zeiss, A. 1964. The Kimmeridgian–Portlandian boundary. In *Colloque du Jurassique, Luxembourg* 1962. *Volume des comptes rendus et mémoires*, Luxembourg : 933–936.

Cope, J. C. W. & Zeiss, A. 1964. Zur Parallelisierung den englischen Oberkimmerdige mit dem fränkischen Untertithon (Malm Zeta). *Geol. Bl. Nordost-Bayern*, Erlangen, **14** : 5–14.

Dacqué, E. 1905. Beitrage zur Geologie des Somalilandes. 2 Oberer Jura. *Beitr. Paläont. Geol. Öst.-Ung.*, Wien, **17** : 119–160, pls. 14–18.

Damon, R. 1884. *Geology of Weymouth, Portland, and the coast of Dorsetshire, from Swanage to Bridport-on-the-Sea: with natural history and archaeological notes.* 2nd (revised) ed. xii + 250 pp. London.

—— 1888. *A supplement to the Geology of Weymouth.* 2nd. (revised) ed. 20 pls. London.

Donovan, D. T. 1957. The Jurassic and Cretaceous Systems in East Greenland. *Meddr. Grønland*, Copenhagen, **155** : 1–214, pls. 1–4.

Donze, P. & Enay, R. 1961. Les céphalopodes du Tithonique inférieur de la Croix-de-Saint-Concors près Chambéry (Savoie). *Trav. Lab. Géol. Univ. Lyon* (n.s.) **7** : 1–236, pls. 1–22.

Douvillé, R. 1910. Un *Virgatites* du Caucase occidental ; origine méditerranéenne du genre ; *Ataxioceras*, *Pseudovirgatites* et *Virgatosphinctes*. *Bull. Soc. géol. Fr.*, Paris (4) **10** : 730–739, 1 fig.

Dumortier, E. & Fontannes, F. 1876. *Description des ammonites de la zone à Ammonites tenuilobatus de Crussol (Ardèche) et de quelques autres fossiles jurassiques nouveaux ou peu connus.* 159 pp., 19 pls. Paris.

Dutertre, A. P. 1926. Contribution à l'étude paléontologique du Portlandien du Boulonnais. *Annls Soc. géol. N.*, Lille, **51** : 240–249.

—— 1927. Remarques sur la position stratigraphique de quelques ammonites du Portlandien moyen du Boulonnais. *C. r. somm. Séanc. Soc. géol. Fr.*, Paris (4) **27** : 36–37.

Favre, E. 1877. La zone à *Ammonites acanthicus* dans les Alpes de la Suisse et de la Savoie. *Abh. schweiz. paläont. Ges.*, Zürich, **4** : 1–112, pls. 1–9.

Frebold, H. 1928. Das Festungsprofil auf Spitzbergen, Jura und Kreide. *Skr. Svalbard Ishavet*, Oslo, **19** : 183–201.

Geyer, O. F. 1961. Über die älteste virgatipartite Berippung der Perisphinctidae (Cephalopoda). *Paläont. Z.*, Stuttgart, **35** : 90–94.

—— 1961*a*. Monographie der Perisphinctidae des unteren Unter-Kimeridgium (Weisser Juraγ, Badenerschichten) im süddeutschen Jura. *Palaeontographica*, Stuttgart, **117**, A : 1–157, pls. 1–22.

Glangeaud, P. 1897. Sur la forme de l'ouverture de quelques ammonites. *Bull. Soc. géol. Fr.*, Paris (3) **25** : 99–107.

Hahn, W. 1963. Die Gattung *Gravesia* Salfeld im Oberjura Mittel—und Nordwesteuropas. *Palaeontographica*, Stuttgart, **122**, A : 90–110, pls. 9–13.

Hölder, H. 1961. Uber den *Ammonites ulmensis* Oppel. *Jber. Mitt. oberrhein. geol. Ver.*, Stuttgart, **43** : 113–117, pl. 5.

Hudleston, W. H. 1896. *In* Hudleston, W. H. Mansel, O. L. & Monckton, H. W. Excursion to Swanage, Corfe Castle, Kimeridge, etc. *Proc. Geol. Ass.*, London, **14**, 312–323.

Ilovaisky, D. & Florensky, K. P. 1941. Les ammonites du Jurassique supérieur des bassins des rivières Oural et Ilek. *Contrib. Connaiss. géol. U.R.S.S., Soc. Nat. Moscou* (n.s.) **5** : 1–195, pls. 1–28. (In Russian).

International Commission for Zoological Nomenclature. 1961. *International Code of Zoological Nomenclature adopted by the 15th. International Congress of Zoology.* xvii + 176 pp. London.

Kerr, J. C. 1895. On some points of the anatomy of *Nautilus pompilius*. *Proc. zool. Soc. Lond.*, **65** : 1–3.

Lamplugh, G. W., Kitchin, F. L. & Pringle, J. 1923. *The concealed Mesozoic rocks in Kent.* iv + 248 pp., 2 pls. (Mem. geol. Surv. U.K., London).

Lane, F. W. 1957. *The Kingdom of the Octopus.* xx + 287 pp., 48 pls., London.

Lewinsky, J. 1922–1923. Monographie géologique et paléontologique du Bononien de la Pologne. *Mém. Soc. géol. Fr.*, Paris, **24–25** : 1–108, pls. 1–11.

Linsley, E. G., Mayr, E. & Usinger, R. L. 1953. *Methods and principles of systematic zoology.* ix + 328 pp., 14 tables, 45 figs., New York.

Makowski, H. 1962. The problem of sexual dimorphism in ammonites. *Palaeont. pol.*, Warsaw, **12** : i–viii + 1–92, pls. 1–20.

Medcof, J. C. 1955. Day and night characteristics of spatfall and of behaviour of oyster larvae. *J. Fish. Res. Bd. Can.*, Ottawa, **12** : 270–286.

Mikhailov, N. P. 1964. Boreal late Jurassic cephalopods. *Trudȳ. geol. Inst. Leningr.*, Moscow, **107** : 1–88, pls. 1–20. (In Russian).

Munier-Chalmas, E. C. P. A. 1892. Sur la possibilité d'admettre un dimorphism sexuel chez les ammonitides. *C. r. somm. Séanc. Soc. géol. Fr.*, Paris (3) **20** : 170–174.

Neaverson, E. 1924. The zonal nomenclature of the Upper Kimmeridge Clay. *Geol. Mag.*, London, **61** : 146–151.

—— 1925. Ammonites from the Upper Kimmeridge Clay. *Pap. geol. Dep. Univ. L'pool.*, **1** : 1–52, pls. 1–4.

Orbigny, A. D'. 1842–1851. *Paléontologie Française, Terrains Jurassiques,* **1**. 642 pp., 234 pls. Paris.

Oppel, A. 1862–1863. Über jurassische Cephalopoden. *Pal. Mitt. Mus. k. Bayer. St.*, Stuttgart, **1** : 127–266, pls. 40–74.

Pavlow, A. P. 1896. On the classification of the strata between the Kimmeridgian and Aptian. *Q. Jl geol. Soc. Lond.*, **52** : 542–555, pl. 27.

Pompeckj, J. 1894. Über Ammonoideen mit anormaler Wohnkammer. *Jh. Ver. vaterl. Naturk. Württ.*, Stuttgart, **49** : 220–290, pl. 4.

Pruvost, P. 1924. Les subdivisions du Portlandien boulonnais d'après les ammonites. *Annls Soc. géol. N.*, Lille, **49** : 187–215, pl. 2.

Pruvost, P. & Pringle, J. 1924. A synopsis of the geology of the Boulonnais, including a correlation of the Mesozoic rocks with those of England. *Proc. Geol. Ass.*, London, **35** : 26–67.

—— 1924*a*. Observations sur la série portlandienne du Boulonnais. *C. r. hebd. Séanc. Acad. Sci. Paris*, **177** : 398–401.

Quenstedt, F. A. 1887–1888. *Die Ammoniten des Schwäbischen Jura.* 3, *Der Weisse Jura* : 817–1140 Atlas pls. 91–126. Stuttgart.

Roll, A. 1932. Stratigraphischer Vergleich zwischen nordwesteuropäischen und süddeutschen oberen Malm. *Neues Jb. Miner. Geol. Paläont. BeilBd.*, Stuttgart, **68**, B : 179–198.

—— 1933. Über den oberen Malm des südwestlichen Frankenalb. *Zentbl. Miner. Geol. Paläont.*, Stuttgart, **10**, B : 553–564.

Rollier, L. 1913. Sur quelques ammonoides jurassiques et leur dimorphisme sexuel. *Archs. Sci. phys. nat.*, Genève (4) **35** : 263–268.

Salfeld, H. 1913. Certain Upper Jurassic strata of England. *Q. Jl geol. Soc. Lond.*, **69** : 423–432, pls. 41, 42.

—— 1914. Die Gliederung des oberen Jura in Nordwesteuropa. *Neues Jb. Miner. Geol. Paläont.*, Stuttgart, **37** : 125–246, 2 figs.

SAUVAGE, H. E. 1911. Sur quelques ammonites du Jurassique supérieur du Boulonnais. *Bull. Soc. géol. Fr.*, Paris (4) **11** : 455–462.

SCHENK, E. T. & MCMASTERS, J. H. 1948. *Procedure in Taxonomy.* 2nd (revised) ed. vii + 93 pp. Stanford & London.

SCHINDEWOLF, O. H. 1925. Entwurf einer Systematik der Perisphincten. *Neues Jb. Miner. Geol. Paläont. BeilBd.*, Stuttgart, **52**, B : 309–343.

—— 1926. Zur Systematik der Perisphincten. *Neues Jb. Miner. Geol. Paläont. BeilBd.*, Stuttgart, **55**, A : 495–517, pl. 19.

SCHNEID, T. 1914–1915. Die Geologie der fränkischen Alb zwischen Eichstätt und Neuberg a.D. *Geogn. Jh.*, München, **27–28** : 59–229, pls. 1–9.

—— 1915. Die Ammonitenfauna der Obertithonisches Kalke von Neuberg a.D. *Geol. paläont. Abh.*, Jena (N.F.) **13** : 305–416, pls. 17–29.

SEILACHER, A. 1960. Epizoans as a key to ammonoid ecology. *J. Paleont.*, Tulsa, **34** : 189–193.

SPATH, L. F. 1923. On ammonites from New Zealand. Appendix to Trechman : The Jurassic of New Zealand. *Q. Jl geol. Soc. Lond.*, **79** : 286–312, pls. 12–18.

—— 1925. The collection of fossils and rocks from Somaliland made by Messrs. Wyllie and Smellie, 7. Ammonites and aptychi. *Monogr. geol. Dep. Hunter. Mus.*, Glasgow, **1** : 111–164, pls. 14, 15.

—— 1927–1933. Revision of the Jurassic cephalopod fauna of Kachh (Cutch), 1–6. *Palaeont. indica,* Calcutta (n.s.) **9**, 2. vii + 955 pp., 130 pls.

—— 1935. The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land, 1. Oxfordian and Lower Kimmeridgian. *Meddr. Grønland,* Copenhagen, **99**, 2 : 1–82, pls. 1–15.

—— 1936. The Upper Jurassic invertebrate faunas of Cape Leslie, Milne Land, 2. Upper Kimmeridgian and Portlandian. *Meddr. Grønland,* Copenhagen, **99**, 3 : 1–180, pls. 1–50.

STENZEL, H. B. 1964. Living Nautilus. In *Treatise on Invertebrate Palaeontology.* Part K. Mollusca 3. (Ed. by R. C. Moore). K59–K93. Kansas & New York.

STRAHAN, A. 1898. *Geology of the Isle of Purbeck.* xi + 278 pp., 11 pls., 183 figs. (Mem. geol. Surv. U.K., London).

TOUCAS, M. A. 1889. Nouvelles observations sur le Jurassique supérieur de l'Ardèche. *Bull. Soc. géol. Fr.*, Paris (3) **17** : 729–742.

—— 1890. Etude de la faune des couches tithoniques de l'Ardèche. *Bull. Soc. géol. Fr.*, Paris (3) **18** : 560–629.

VETTERS, H. 1905. Die Fauna der Juraklippen zwischen Donau und Thaya. *Beitr. Paläont. Geol. Öst.-Ung.*, Wien, **17** : 223–259, pls. 21, 22.

WESTERMANN, G. E. G. 1964. Sexual-Dimorphismus bei Ammonoideen und seine Bedeutung für die Taxionomie der Otoitidae. *Palaeontographica*, Stuttgart, **124**, A : 33–73, pls. 6–9.

WILLEY, A. 1897. The oviposition of *Nautilus macromphalus*. *Proc. R. Soc.*, London, **60**: 467–471.

—— 1897*a*. Adhesive tentacles of *Nautilus*, with some notes on its pericardium and spermatophores. *Q. Jl microsc. Sci.*, London, **40** : 207–209, pl. 2.

—— 1899. Some zoological results of a voyage to Melanesia during the years 1894–1897. *Proc. Camb. phil. Soc.*, London, **9**, 8 : 397–400.

—— 1902. *Zoological results based on material from New Britain, New Guinea, Loyalty Islands and elsewhere.* 6. *Contribution to the natural history of the Pearly Nautilus* : 691–826, pls. 75–83. Cambridge.

YONGE, C. M. 1960. *Oysters.* xiv + 209 pp., 17 pls. London.

ZIEGLER, B. 1962. Die Ammoniten-Gattung *Aulacostephanus* im Oberjura. *Palaeontographica*, Stuttgart, **119**, A : 1–172, pls. 1–22.

PLATES

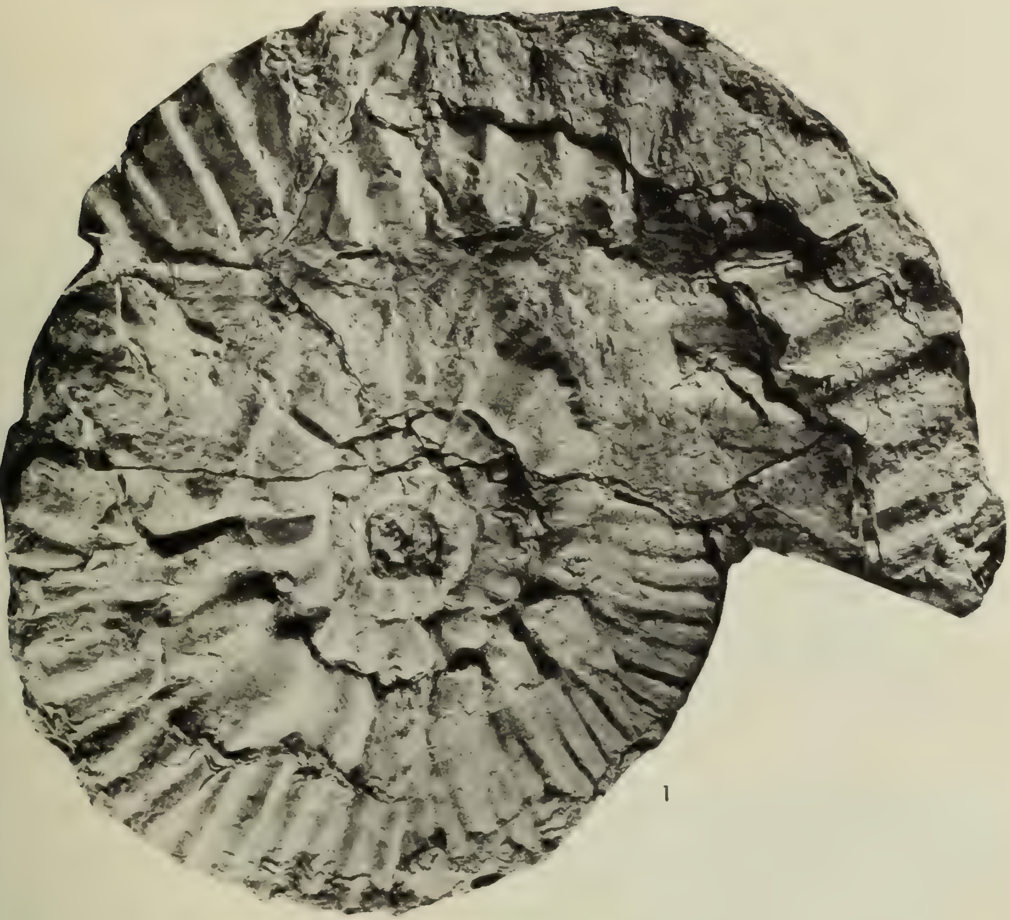
The photographs are by Mr. S. P. Osborn of the Geology Department, University College, Swansea.

All the specimens were whitened with ammonium chloride prior to photographing.

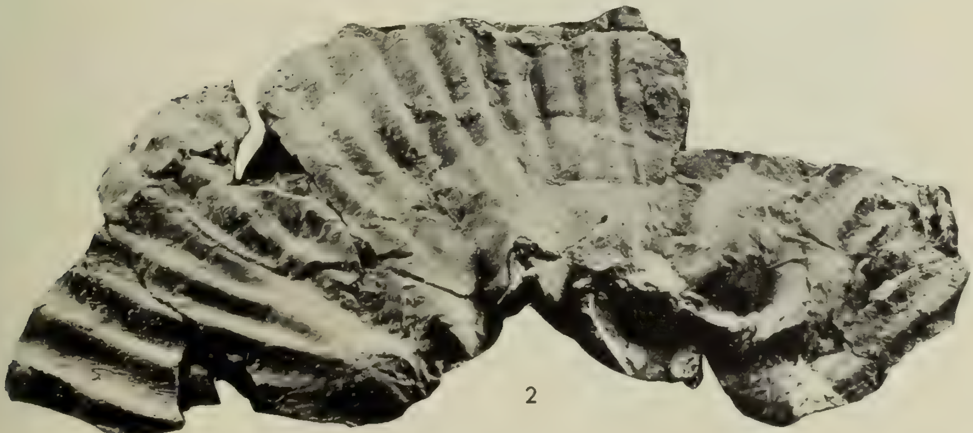
PLATE 1

FIG. 1. ***Gravesia gigas*** (Zieten). C.73390, ×0·45, 45 feet below Yellow Ledge Stone Band.

FIG. 2. ***Gravesia*** cf. ***gravesiana*** (d'Orbigny). C.73391, ×1, 8 feet below Yellow Ledge Stone Band.



1



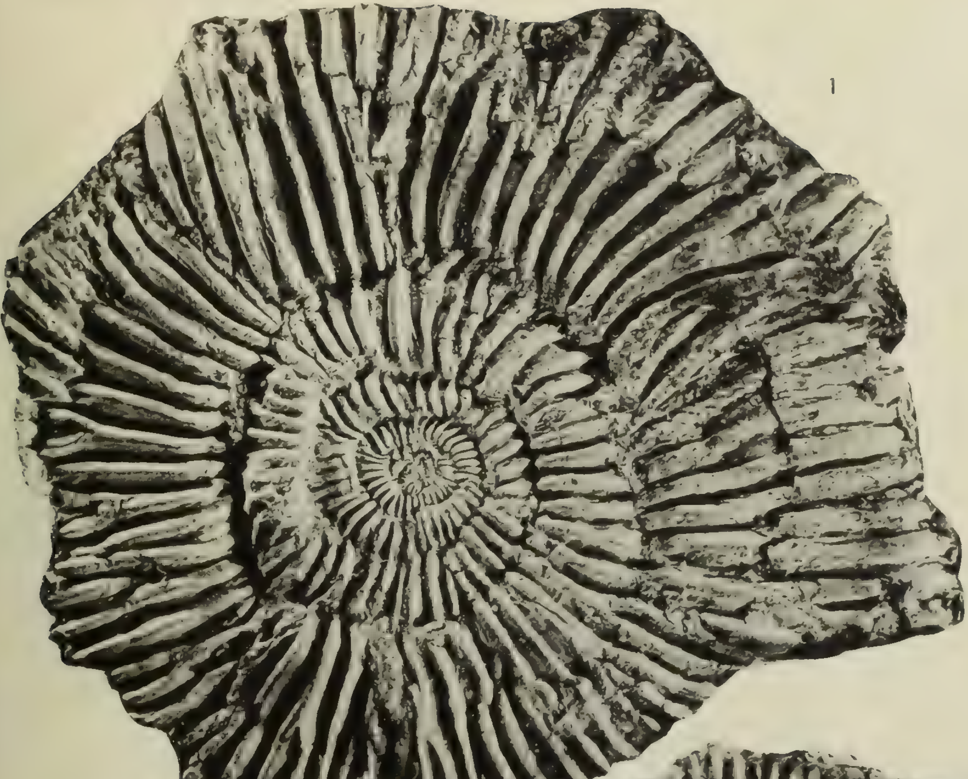
2

PLATE 2

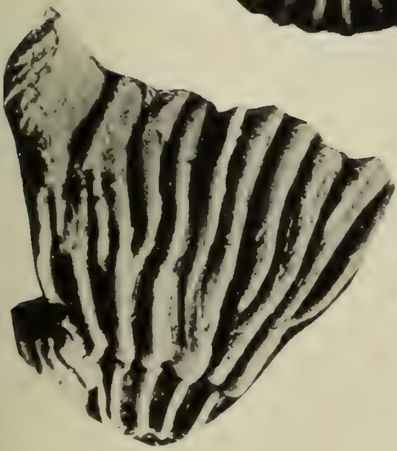
FIG. 1. ***Pectinatites* (*Arkellites*) *primitivus*** sp. nov. Holotype (macroconch), C.73392, ×1, 25 feet below Yellow Ledge Stone Band.

FIG. 2. ***Pectinatites* (*Arkellites*) *primitivus*** sp. nov. Paratype (microconch), C.73395, ×1, 55 feet below Yellow Ledge Stone Band.

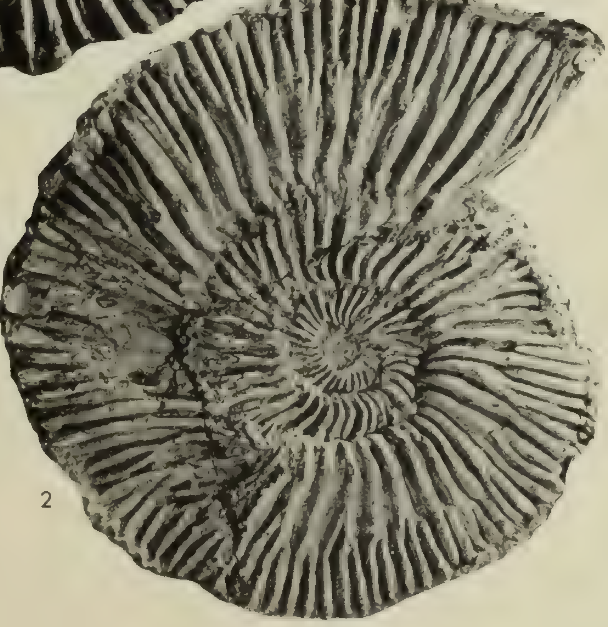
FIG. 3. ***Pectinatites* (*Arkellites*) *hudlestoni*** sp. nov. Microconch, C.73402, ×1·5, ventral view showing possible points of shedding of horns. 13 feet above Rope Lake Head Stone Band.



1



3

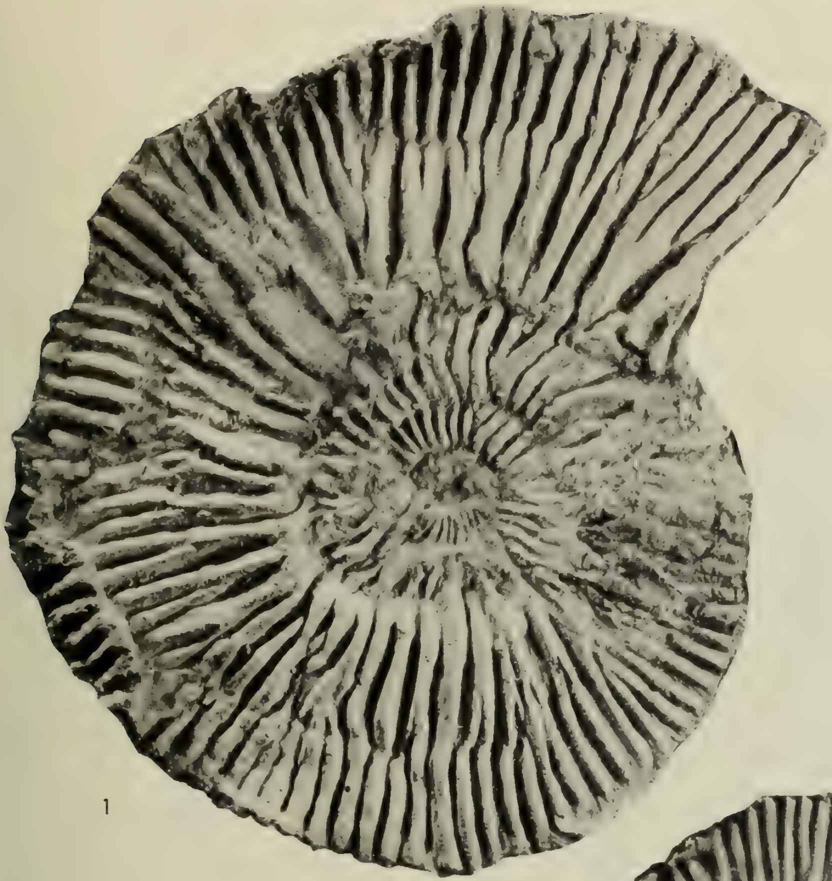


2

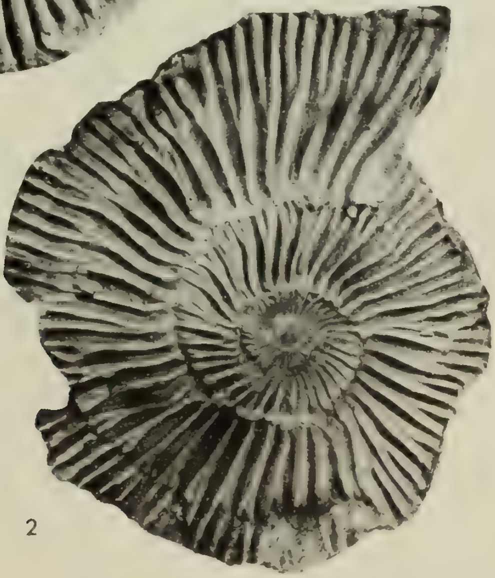
PLATE 3

Fig. 1. ***Pectinatites (Arkellites) primitivus*** sp. nov. Paratype (macroconch), C.73393, × 1, 25 feet below Yellow Ledge Stone Band.

Fig. 2. ***Pectinatites (Arkellites) primitivus*** sp. nov. Paratype (microconch), C.73394, × 1, 25 feet below Yellow Ledge Stone Band.



1



2

PLATE 4

Pectinatites (Arkellites) cuddlensis sp. nov. Holotype (macroconch), C.73396, ×1, 18 feet above Yellow Ledge Stone Band.

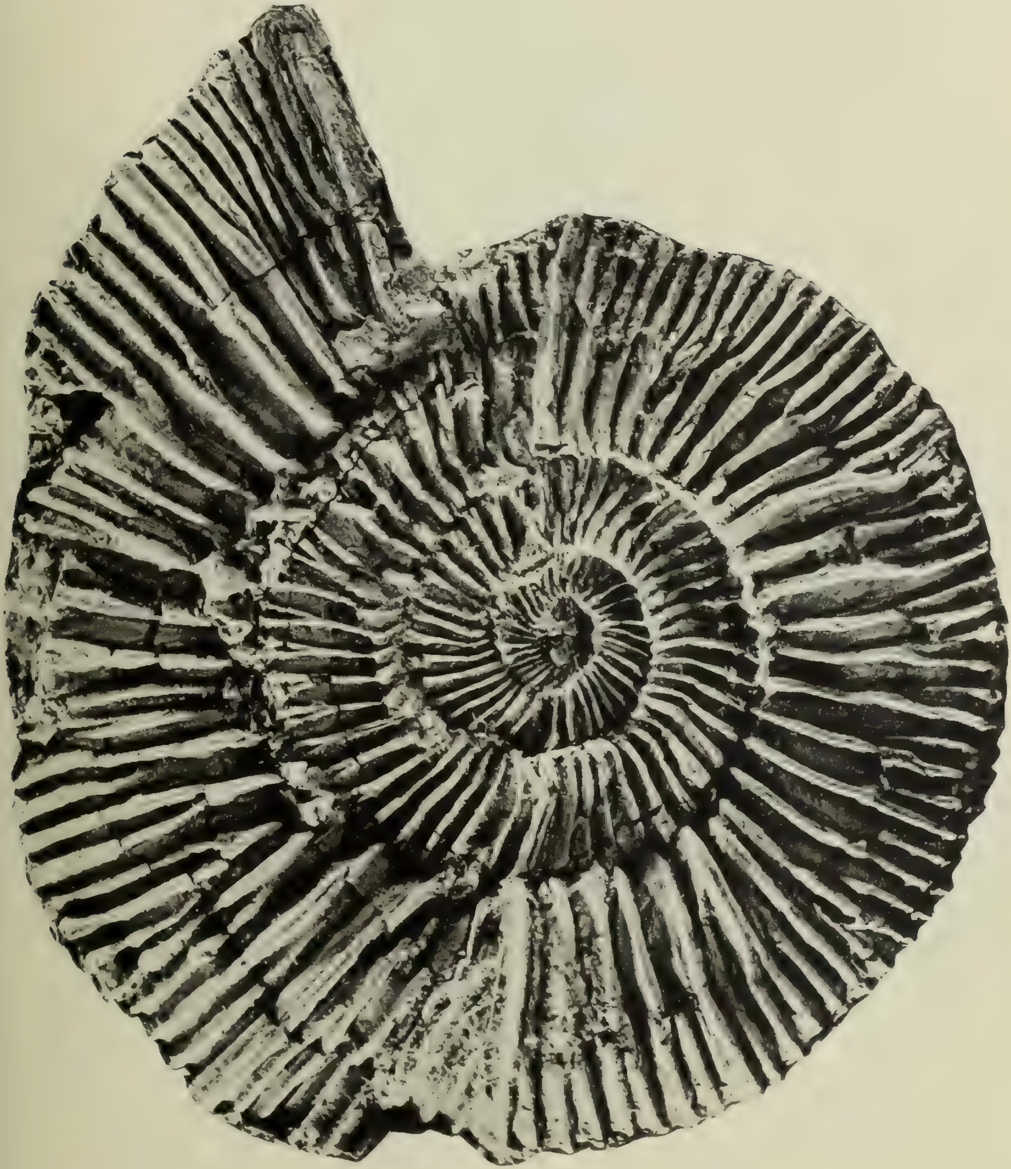
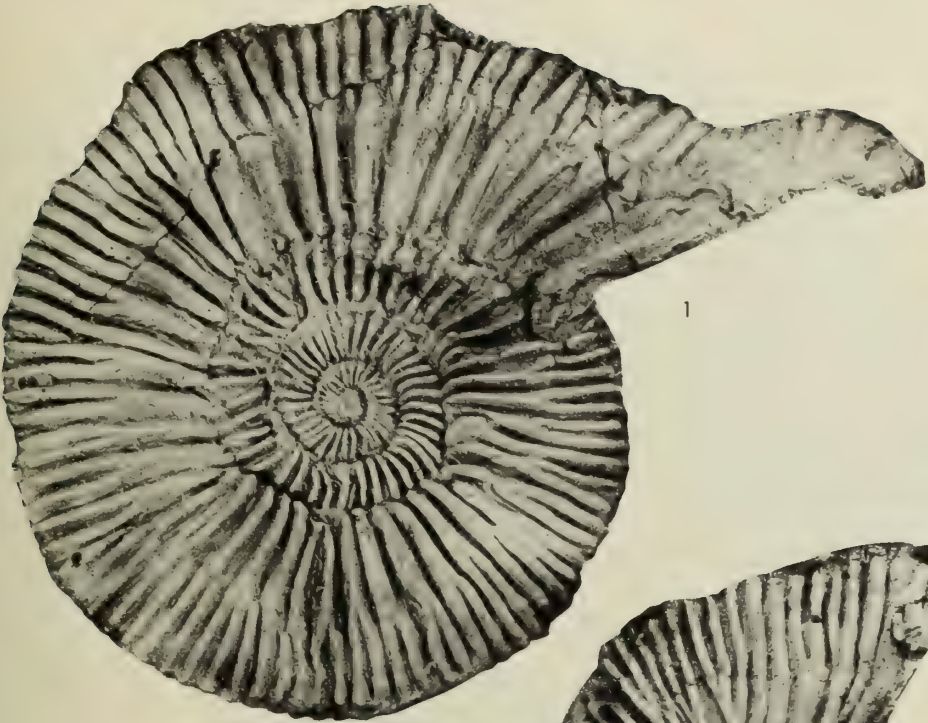


PLATE 5

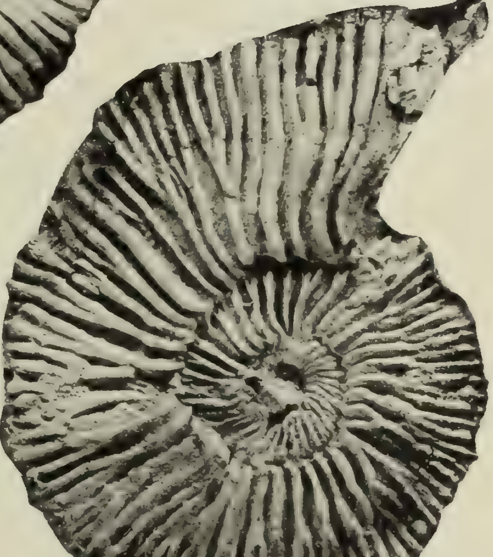
Fig. 1. ***Pectinatites (Arkellites) cuddlensis*** sp. nov. Paratype (microconch), C.73397, × 1, 25 feet above Yellow Ledge Stone Band.

Fig. 2. ***Pectinatites (Arkellites) damoni*** sp. nov. Paratype (microconch), C.73400, × 1, 25 feet above Yellow Ledge Stone Band.

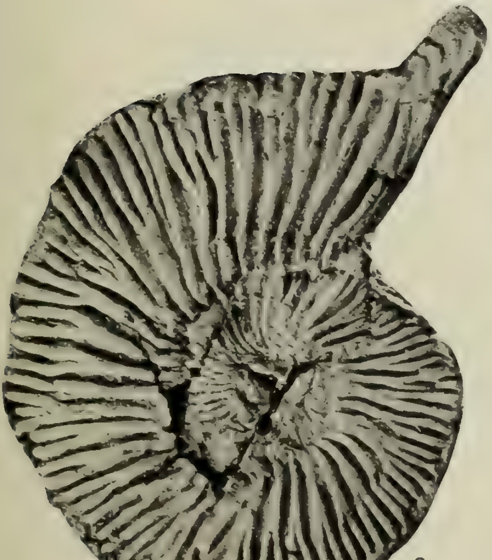
Fig. 3. ***Pectinatites (Arkellites) damoni*** sp. nov. Paratype (microconch), C.73401, × 1, 25 feet above Yellow Ledge Stone Band.



1



2

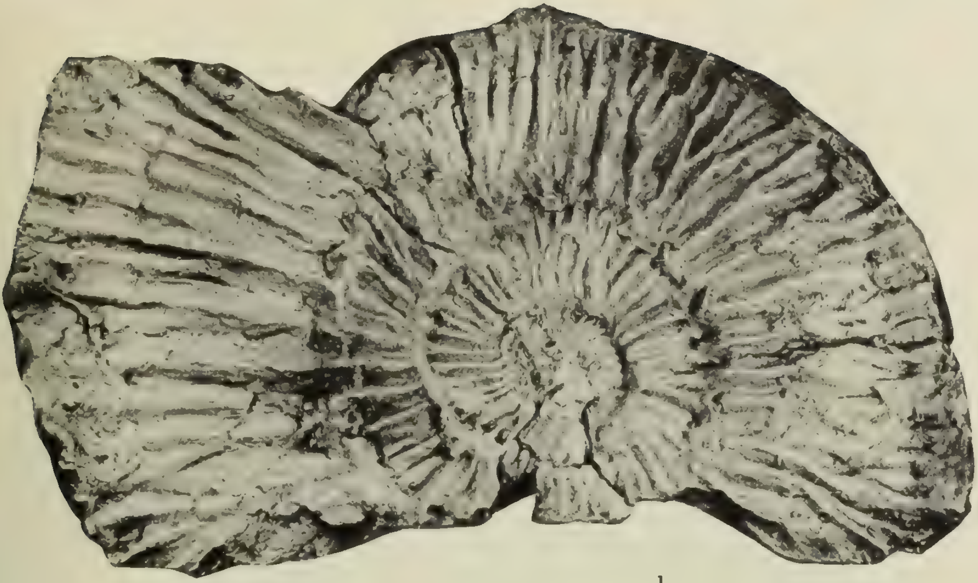


3

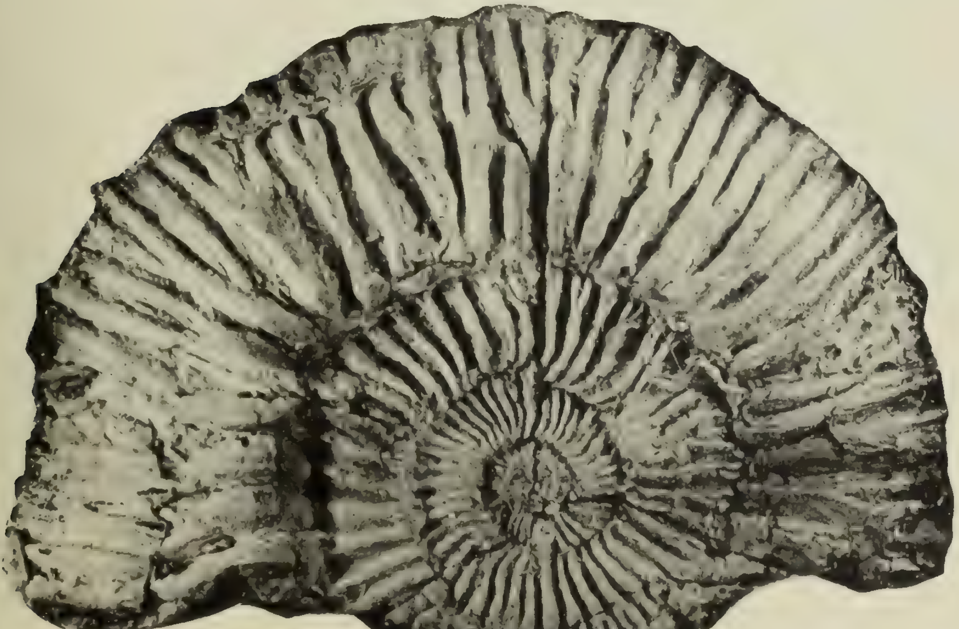
PLATE 6

Fig. 1. ***Pectinatites (Arkellites) damoni*** sp. nov. Paratype (macroconch), C.73399, ×1, 27 feet above Yellow Ledge Stone Band.

Fig. 2. ***Pectinatites (Arkellites) damoni*** sp. nov. Holotype (macroconch), C.73398, ×1, 25 feet above Yellow Ledge Stone Band.



1



2

PLATE 7

Pectinatites* (*Arkellites*) *hudlestoni sp. nov. Holotype (macroconch), C.73403, ×0·85, 13 feet above Rope Lake Head Stone Band.

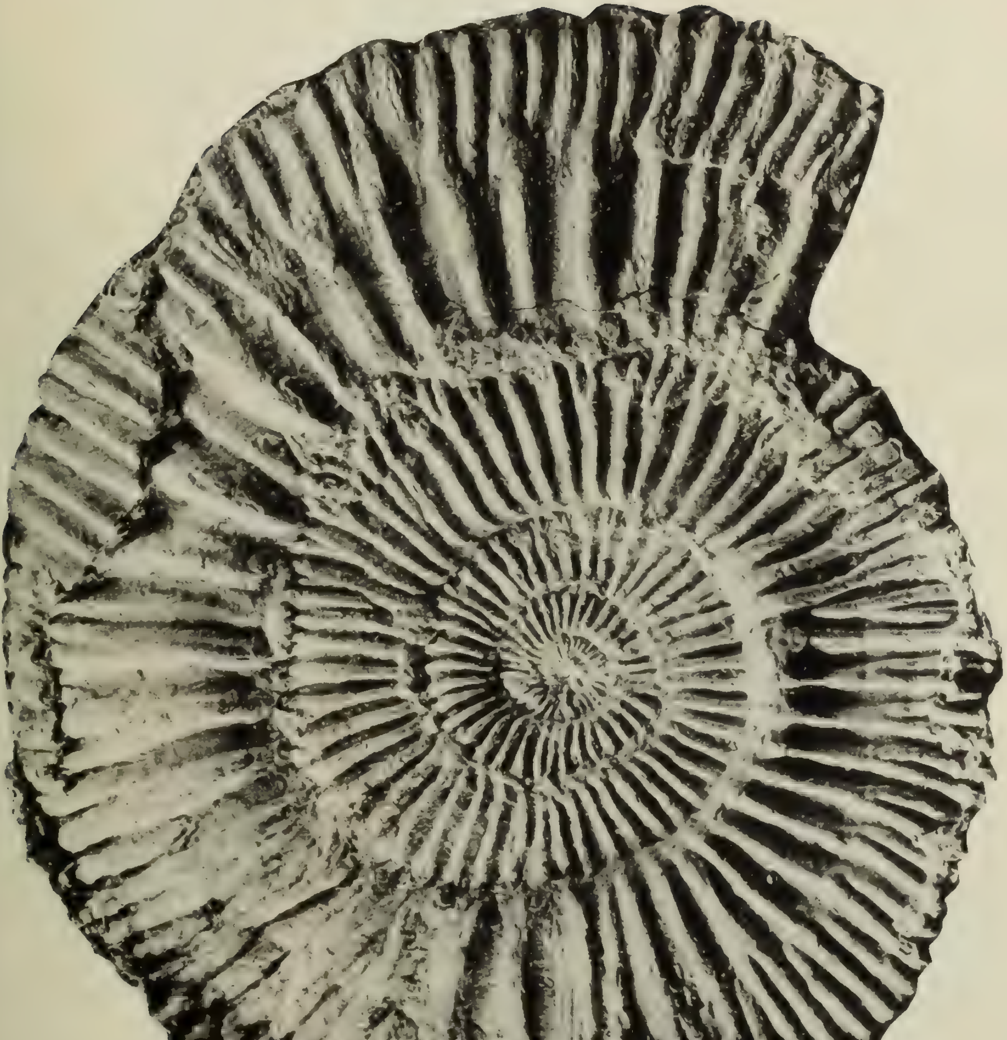
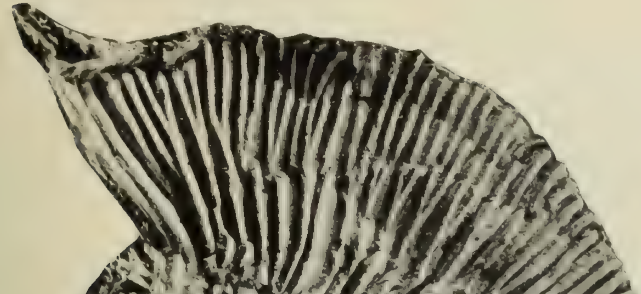


PLATE 8

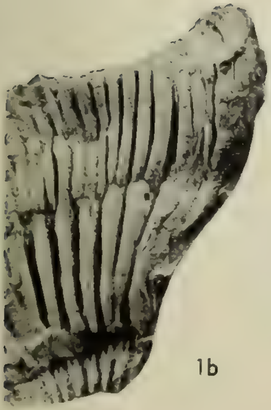
Fig. 1a. ***Pectinatites (Virgatosphinctoides) elegans*** sp. nov. Paratype (microconch), C.73406, × 1, 20 feet below Yellow Ledge Stone Band.

Fig. 1b. Reverse side of specimen in Fig. 1a, showing detail of the peristomal inflation. × 1.

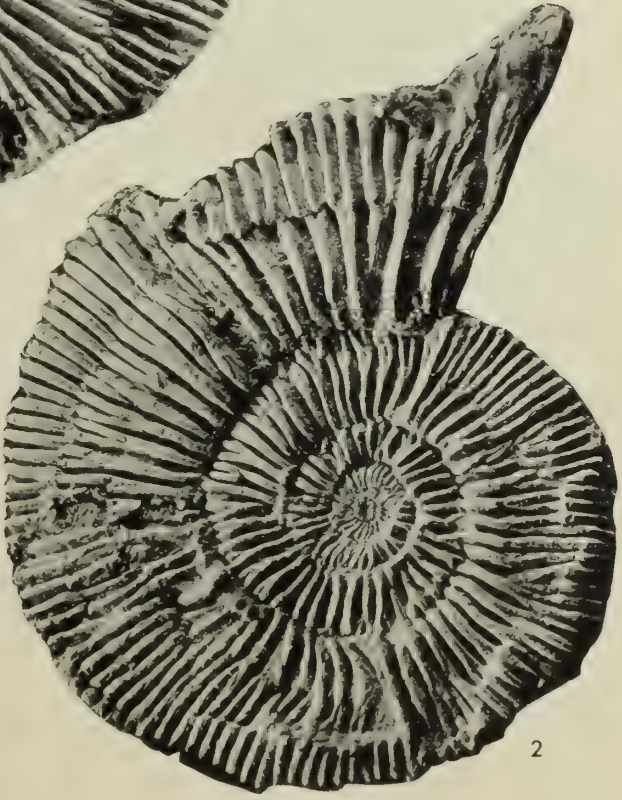
Fig. 2. ***Pectinatites (Arkellites) hudlestoni*** sp. nov. Paratype (microconch), C.73404, × 1, 13 feet above Rope Lake Head Stone Band.



1a



1b



2

PLATE 9

Pectinatites* (*Virgatosphinctoides*) *elegans sp. nov. Holotype (macroconch), C.73405, ×0·95, 18 feet below Yellow Ledge Stone Band.

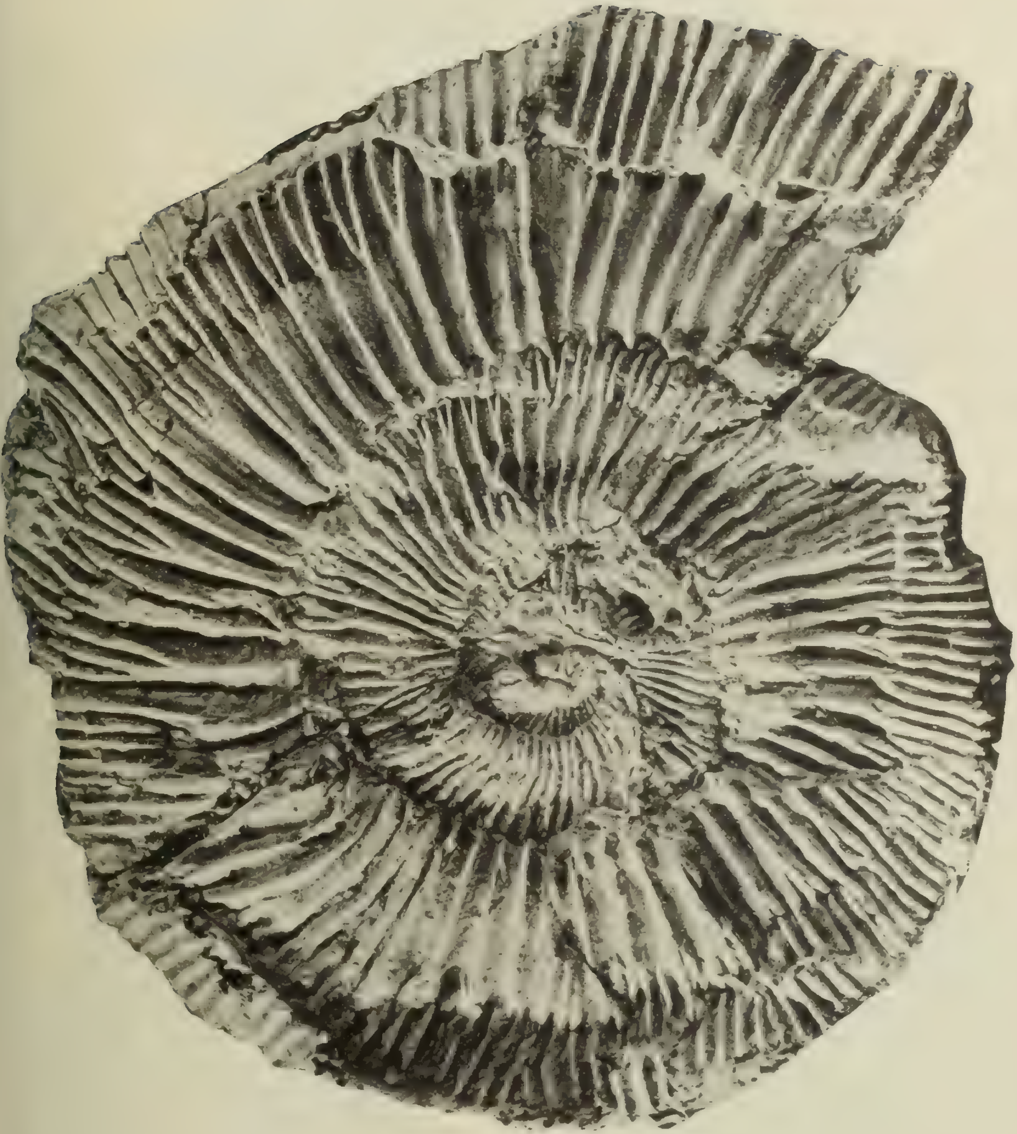


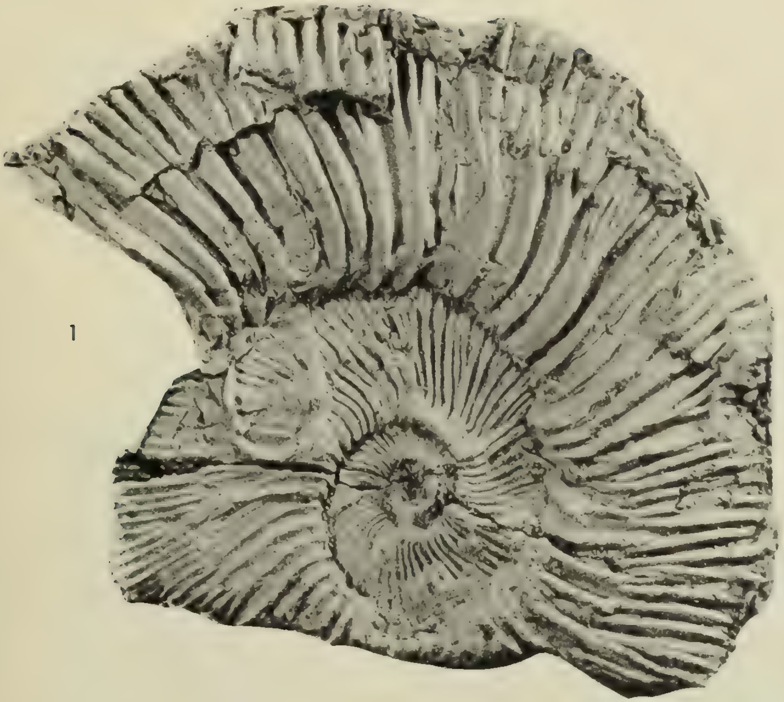
PLATE 10

FIG. 1. ***Pectinatites* (*Virgatosphinctoides*) *elegans corniger*** subsp. nov. Holotype (macroconch), C.73407, × 1, 5 feet below Yellow Ledge Stone Band.

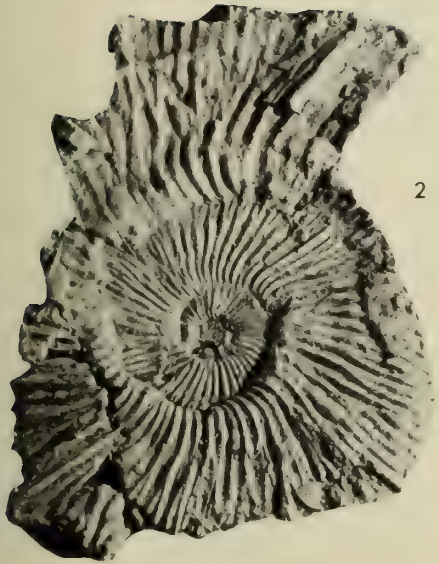
FIG. 2. ***Pectinatites* (*Virgatosphinctoides*) *elegans corniger*** subsp. nov. Paratype (microconch), C.73409, × 1, 8 feet below Yellow Ledge Stone Band.

FIG. 3. ***Pectinatites* (*Virgatosphinctoides*) *elegans corniger*** subsp. nov. Paratype (microconch), C.73408, × 1, 5 feet below Yellow Ledge Stone Band.

1



2



3

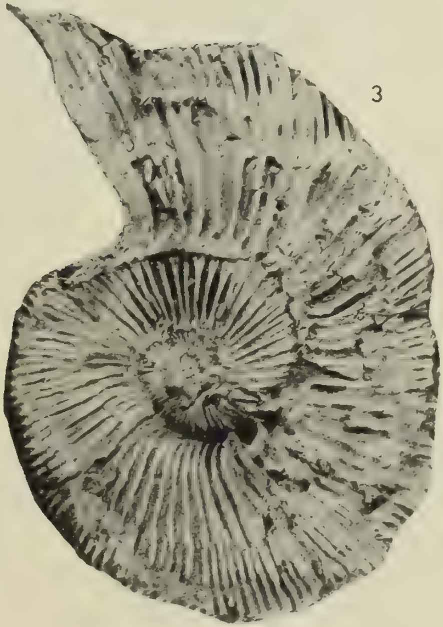
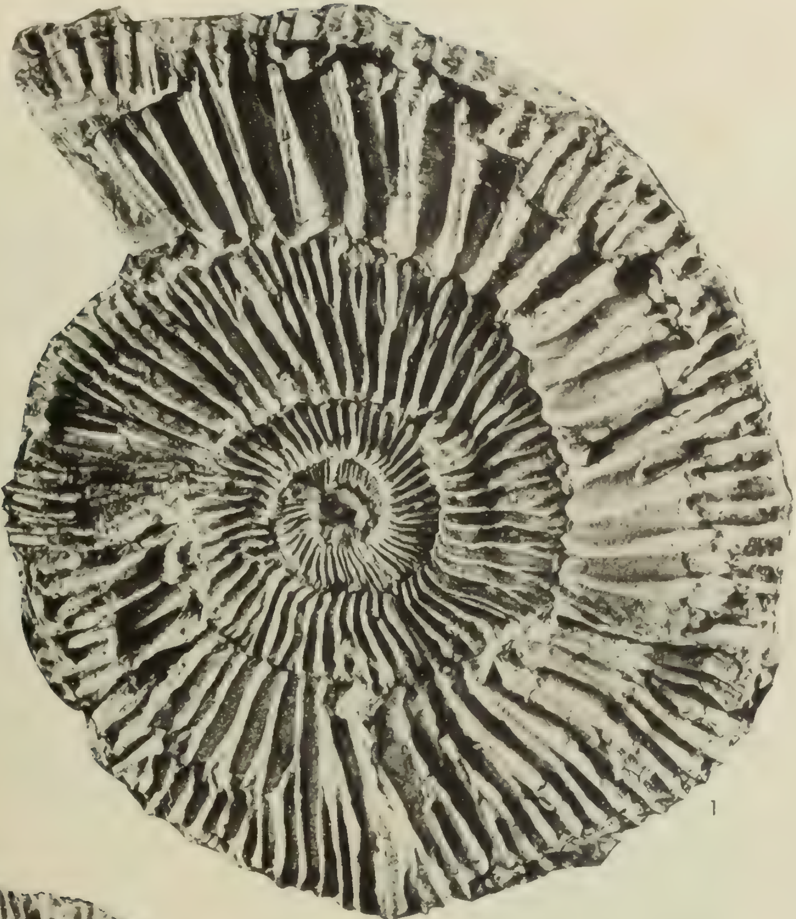


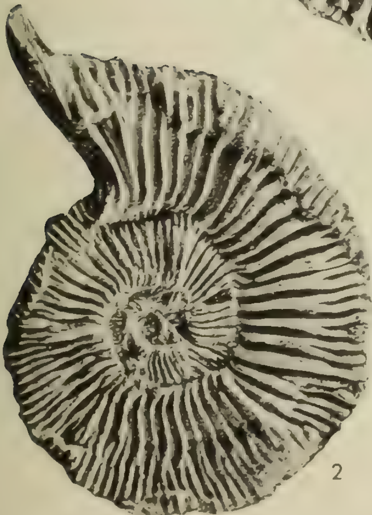
PLATE 11

FIG. 1. ***Pectinatites (Virgatosphinctoides) scitulus*** sp. nov. Holotype (macroconch), C.73411, ×0·85, 24 feet above Yellow Ledge Stone Band.

FIG. 2. ***Pectinatites (Virgatosphinctoides) scitulus*** sp. nov. Paratype (microconch), C.73412, ×0·85, 25 feet above Yellow Ledge Stone Band.

FIG. 3. ***Pectinatites (Virgatosphinctoides) scitulus*** sp. nov. Paratype (microconch), C.73413, ×0·85, 15 feet above Yellow Ledge Stone Band.


1


2

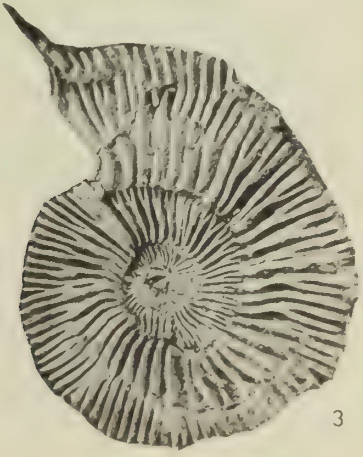
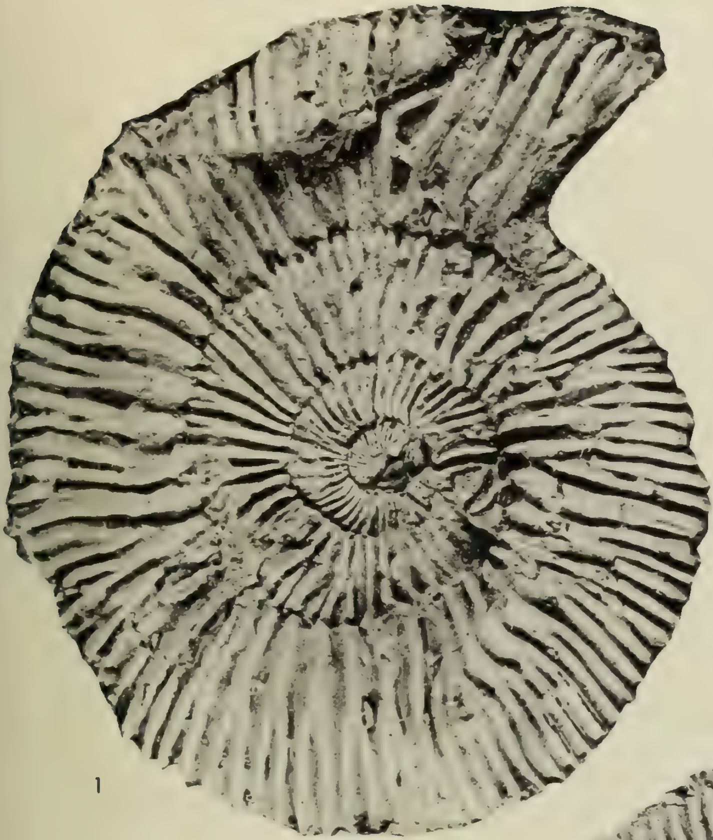

3

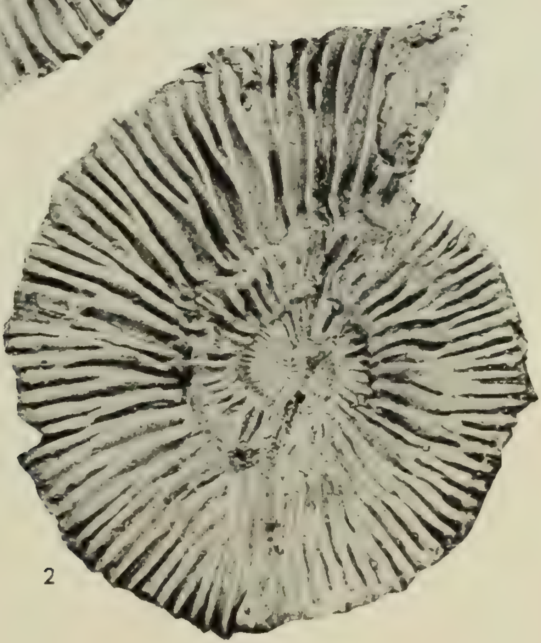
PLATE 12

FIG. 1. ***Pectinatites (Virgatosphinctoides) decorosus*** sp. nov. Holotype (macroconch), C.73414, ×1, 15 feet above Yellow Ledge Stone Band.

FIG. 2. ***Pectinatites (Virgatosphinctoides) decorosus*** sp. nov. Paratype (microconch), C.73415, ×1, 15 feet above Yellow Ledge Stone Band.



1



2

PLATE 13

Pectinatites* (*Virgatosphinctoides*) *major sp. nov. Holotype (macroconch), C.73410, × 0·55, 6 feet below Yellow Ledge Stone Band.

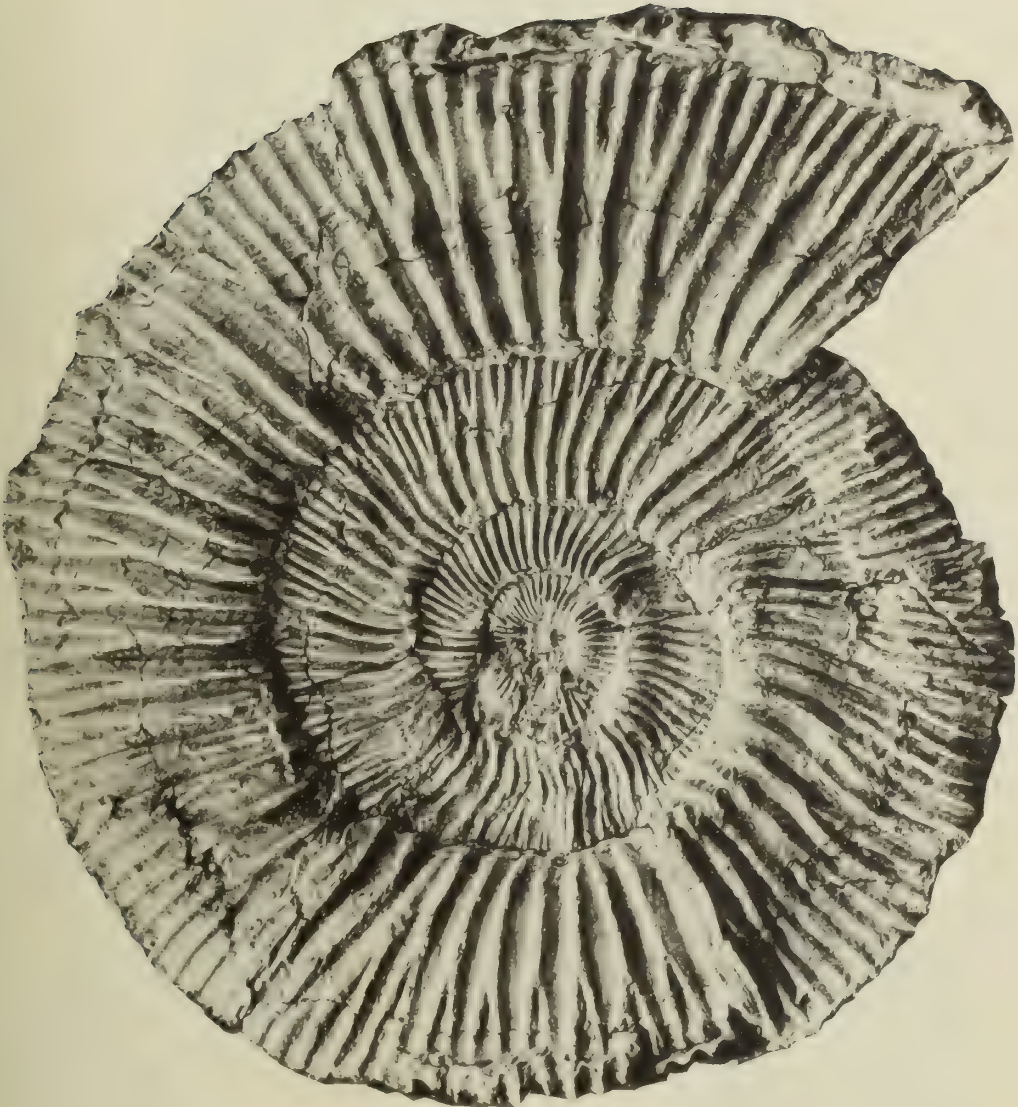
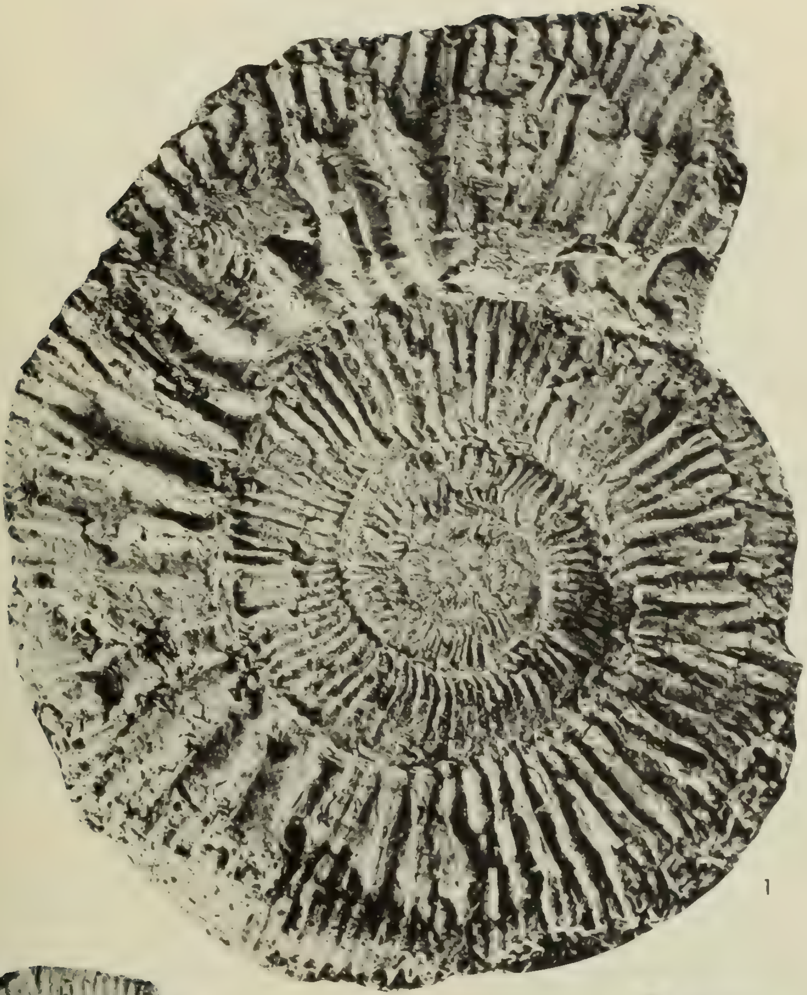


PLATE 14

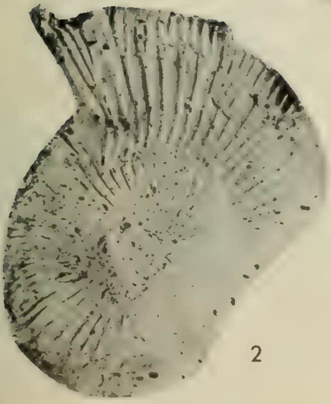
Fig. 1. ***Pectinatites* (*Virgatosphinctoides*) *clavelli*** sp. nov. Holotype (macroconch), C.73432, × 0·7, 8 feet above Grey Ledge Stone Band.

Fig. 2. ***Pectinatites* (*Virgatosphinctoides*) *clavelli*** sp. nov. Paratype (microconch), C.73433, × 0·7, 3 feet above Grey Ledge Stone Band.

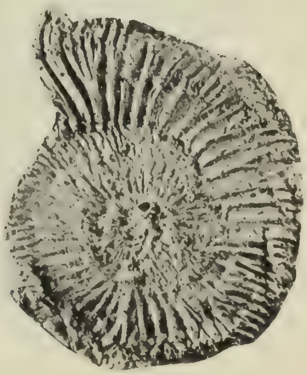
Fig. 3. ***Pectinatites* (*Virgatosphinctoides*) *clavelli*** sp. nov. Paratype (microconch), C.73434, × 0·7, 3 feet above Grey Ledge Stone Band.



1



2



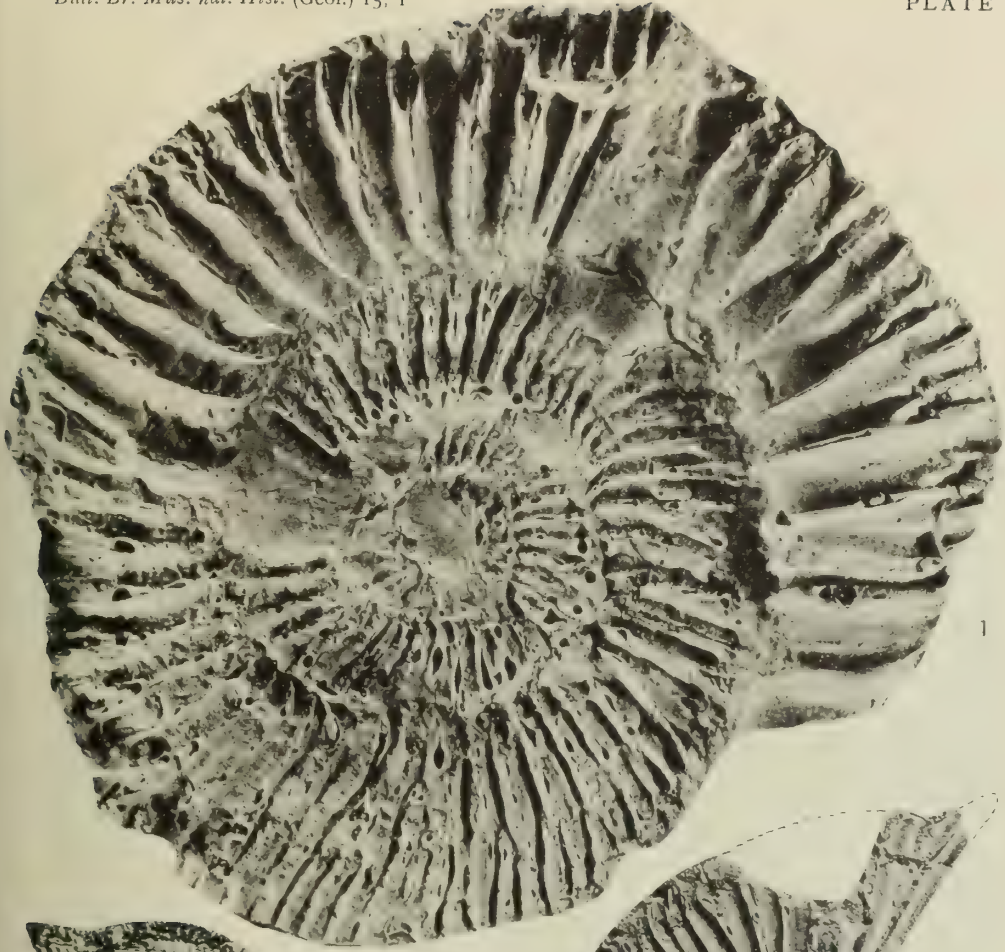
3

PLATE 15

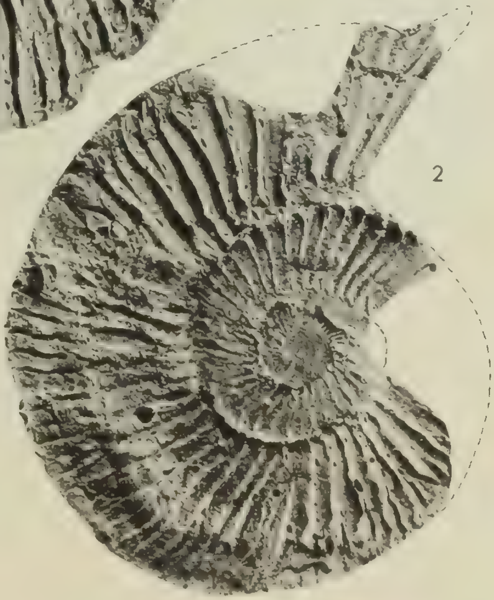
FIG. 1. ***Pectinatites* (*Virgatosphinctoides*) *smedmorensis*** sp. nov. Holotype (macroconch), C.73430, × 1, 22 feet below Blackstone.

FIG. 2. ***Pectinatites* (*Virgatosphinctoides*) *smedmorensis*** sp. nov. Paratype (microconch), C.73431, × 1, 22 feet below Blackstone. The postulated original shell outline indicated by broken lines.

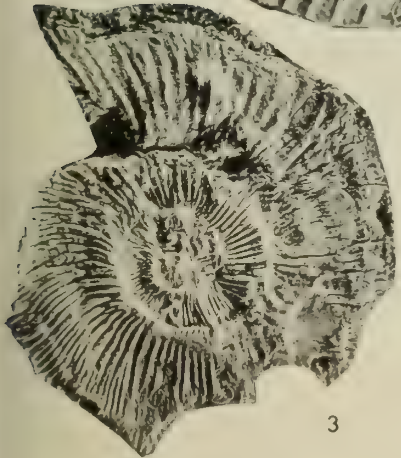
FIG. 3. ***Pectinatites* (*Virgatosphinctoides*) *grandis*** (Neaverson). Microconch, C.73421, × 0·6, 17 feet below Blackstone.



1



2



3

PLATE 16

Pectinatites* (*Virgatosphinctoides*) *laticostatus sp. nov. Holotype (macroconch), C.73416, ×0·65, 19 feet below Blackstone.

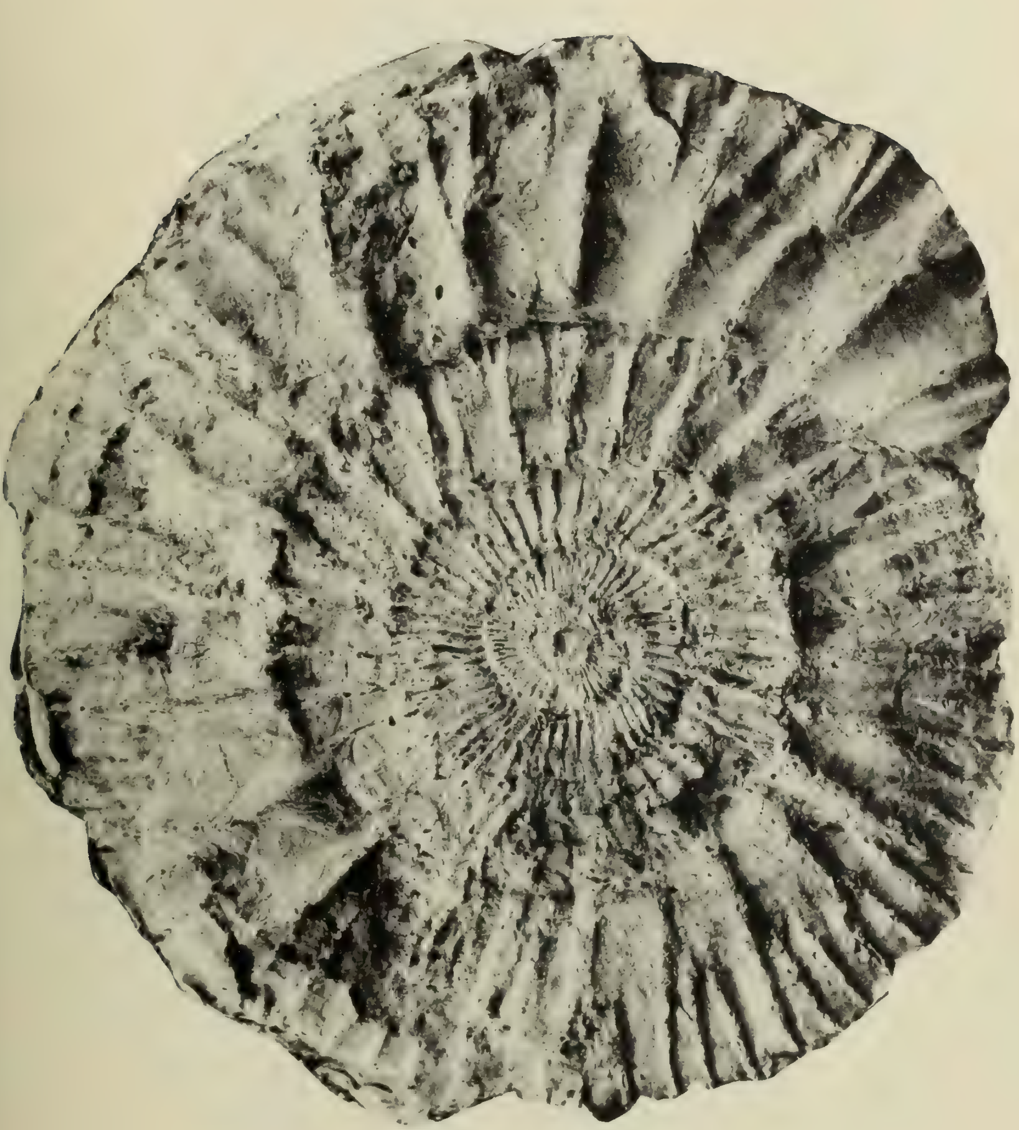


PLATE 17

Pectinatites* (*Virgatosphinctoides*) *pseudoscruposus (Spath). Macroconch, C.73418, ×0·7, 4 feet below Blackstone.

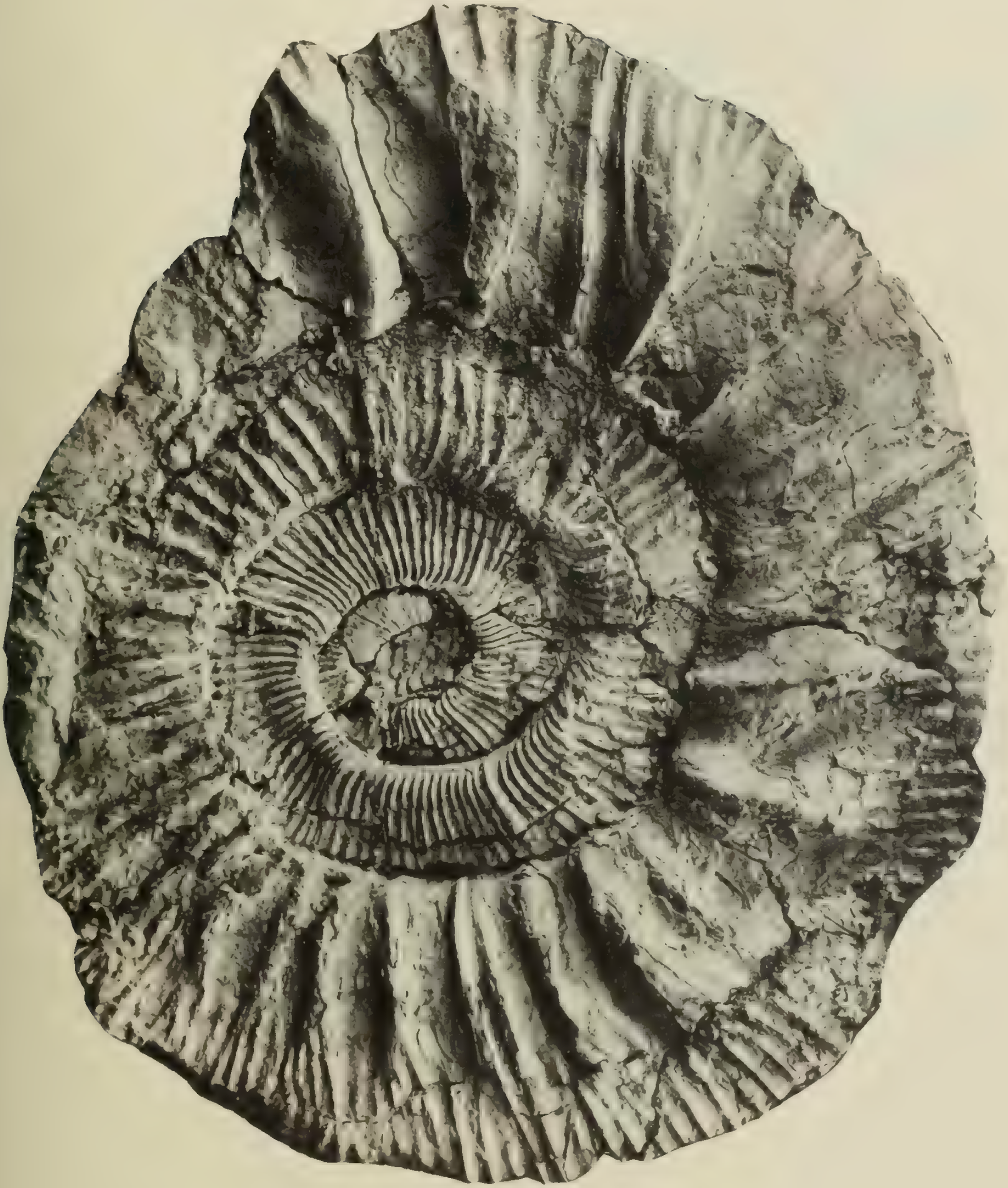


PLATE 18

Pectinatites (Virgatosphinctoides) grandis (Neaverson). Macroconch, C.73420, ×0·45, 4 feet below Blackstone.

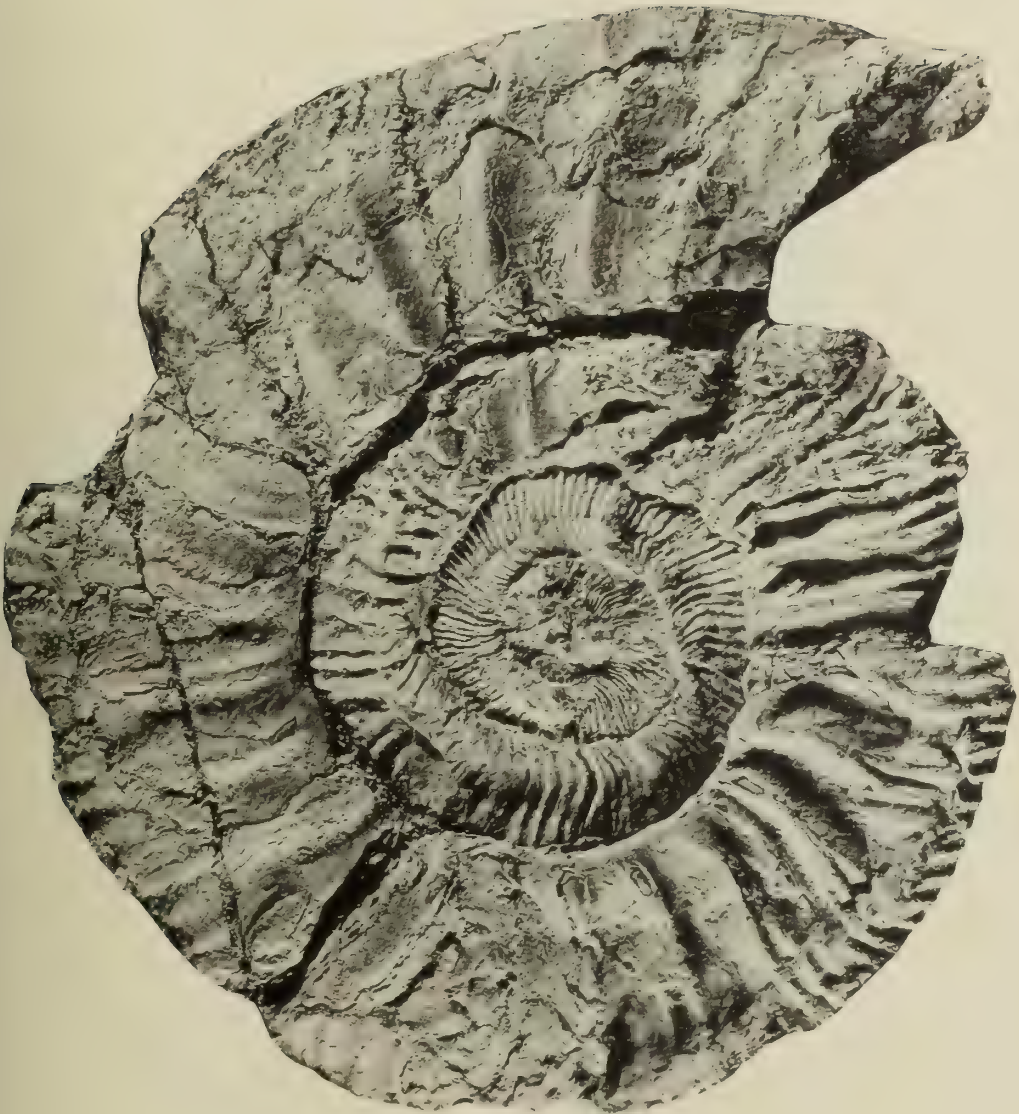


PLATE 19

Pectinatites* (*Virgatosphinctoides*) *grandis acceleratus subsp. nov. Holotype (macroconch), C.73422, ×0·45, 13 feet above Rope Lake Head Stone Band.

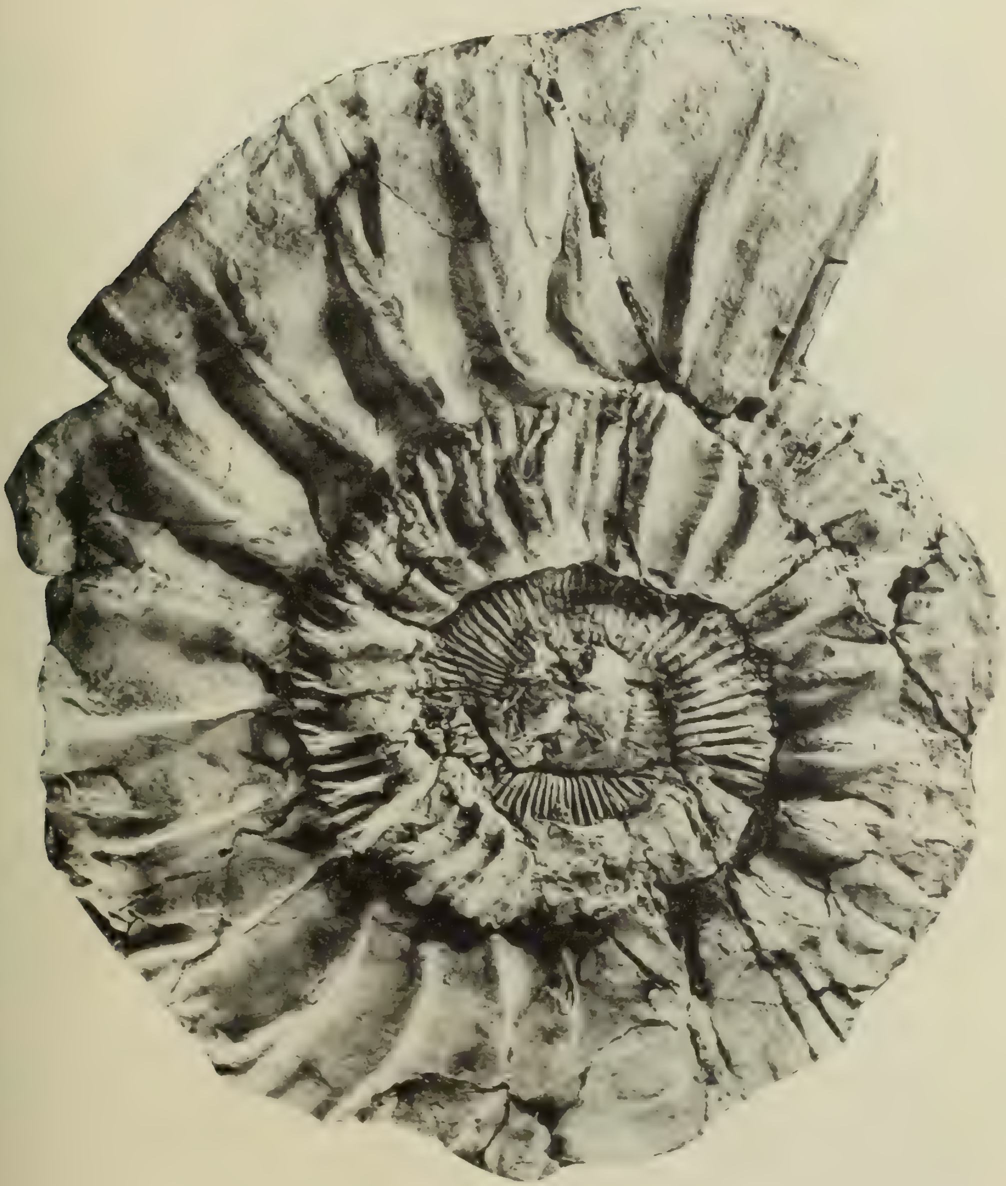
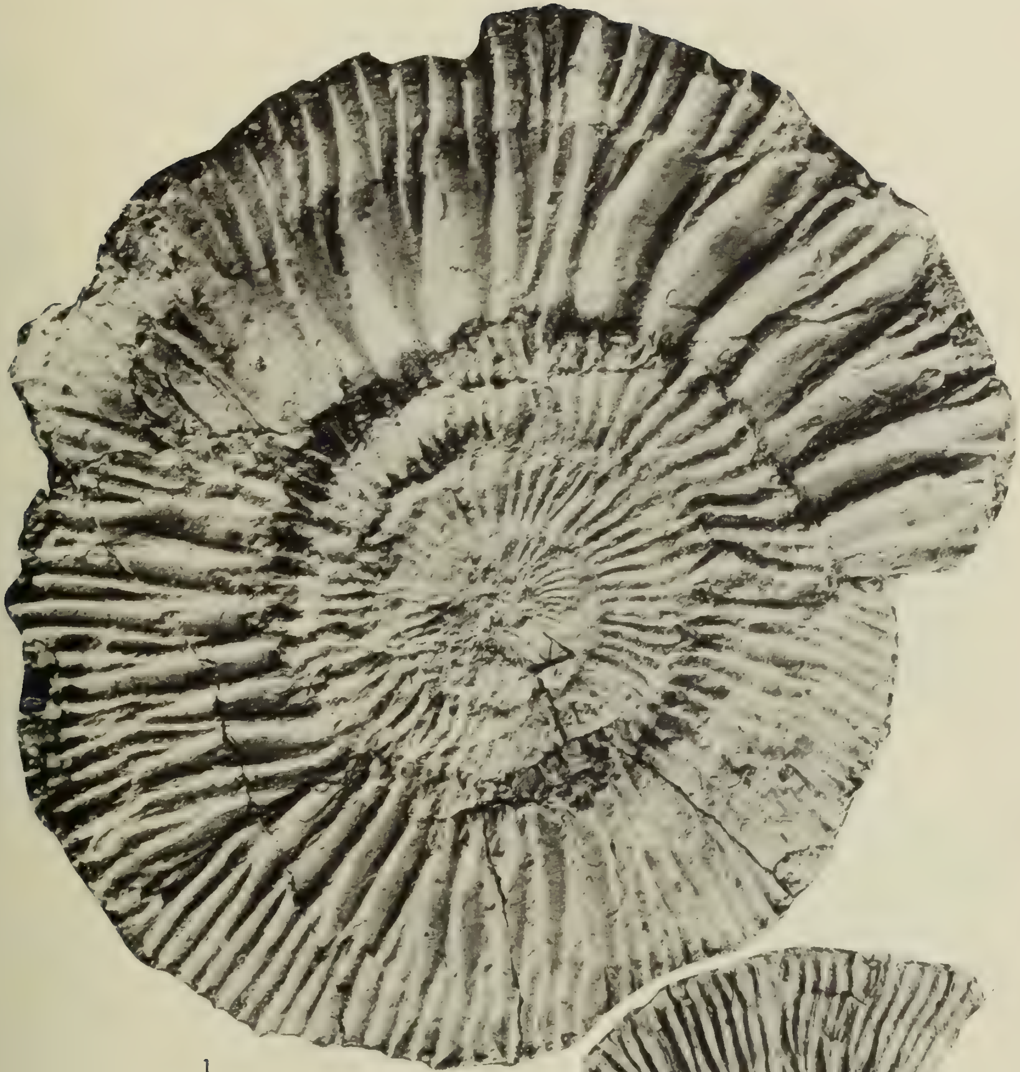


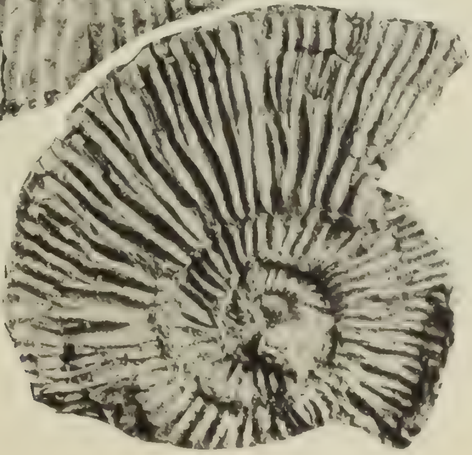
PLATE 20

FIG. 1. ***Pectinatites* (*Virgatosphinctoides*) *woodwardi*** (Neaverson). Macroconch, C.73423, × 1, 15 feet below Blackstone.

FIG. 2. ***Pectinatites* (*Virgatosphinctoides*) *woodwardi*** (Neaverson). Microconch, C.73424, × 1, 15 feet below Blackstone. The postulated original extent of the horn indicated by broken line.



1



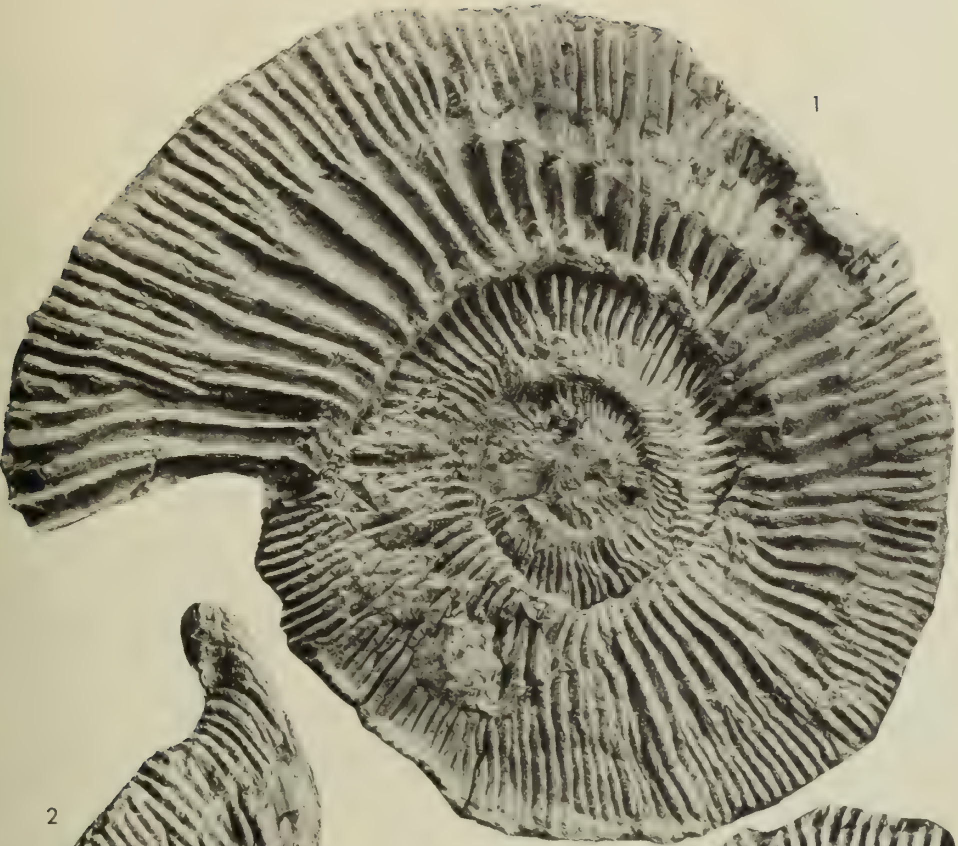
2

PLATE 21

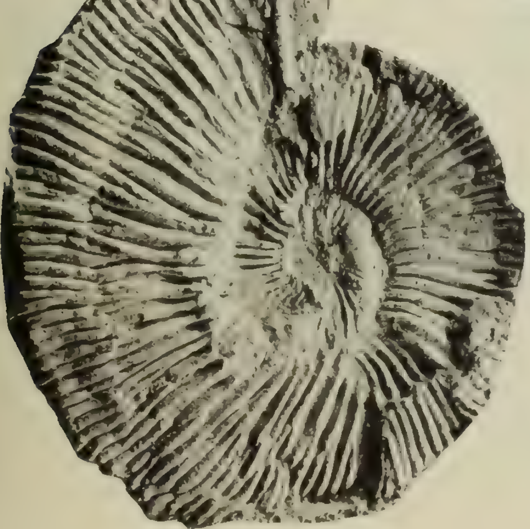
Fig. 1. ***Pectinatites* (*Virgatosphinctoides*) *wheatleyensis*** (Neaverson). Macroconch, C.73425, × 1, 12 feet below Blackstone.

Fig. 2. ***Pectinatites* (*Virgatosphinctoides*) *wheatleyensis*** (Neaverson). Microconch, C.73426, × 1, 12 feet below Blackstone.

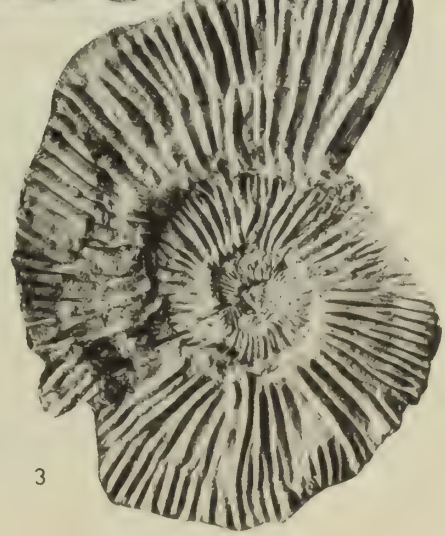
Fig. 3. ***Pectinatites* (*Virgatosphinctoides*) *wheatleyensis*** (Neaverson). Microconch, C.73427, × 1, 15 feet below Blackstone.



1



2



3

PLATE 22

Pectinatites* (*Virgatosphinctoides*) *reisiformis sp. nov. Holotype (macroconch), C.73435, ×1, 13 feet above Rope Lake Head Stone Band.

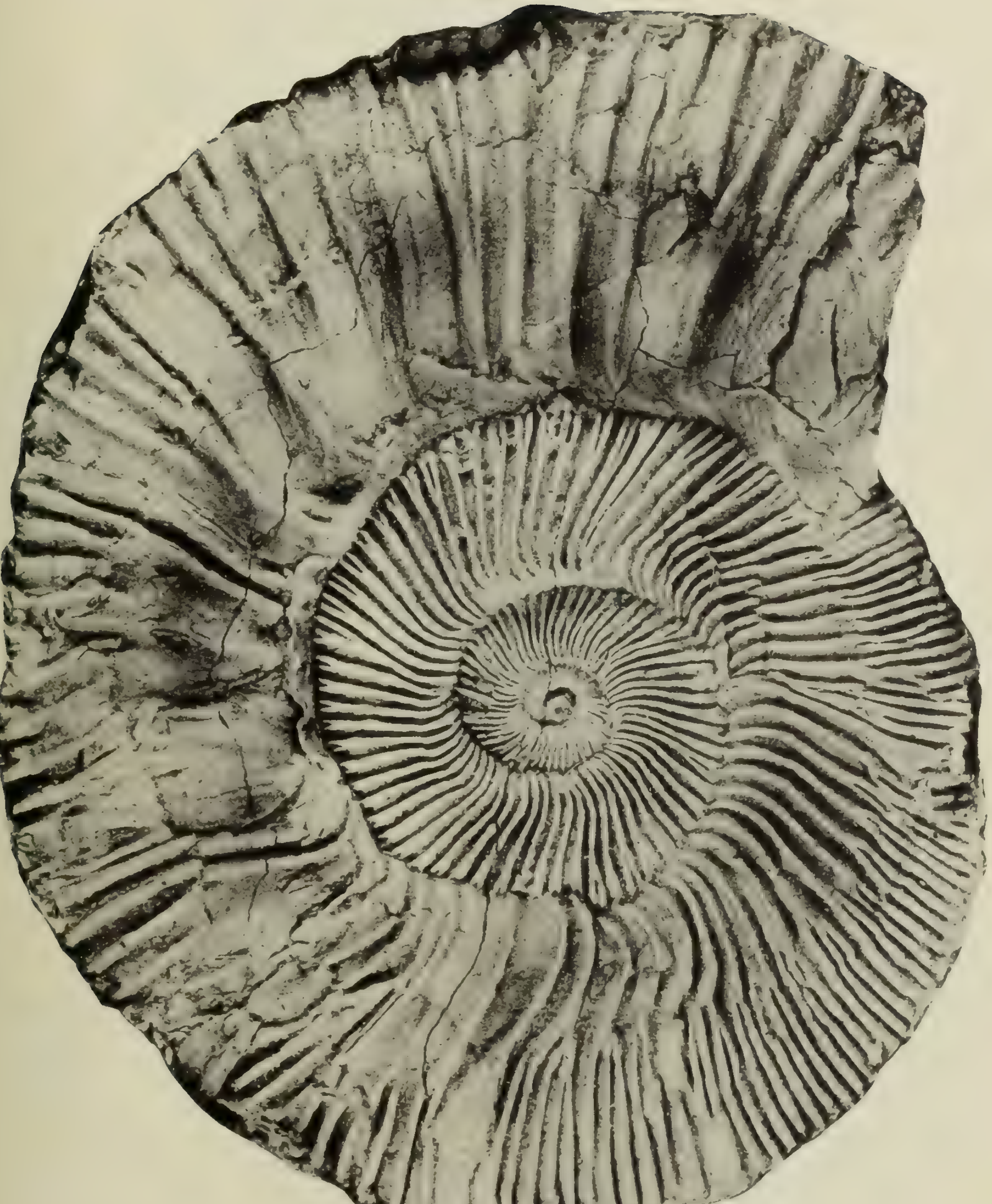
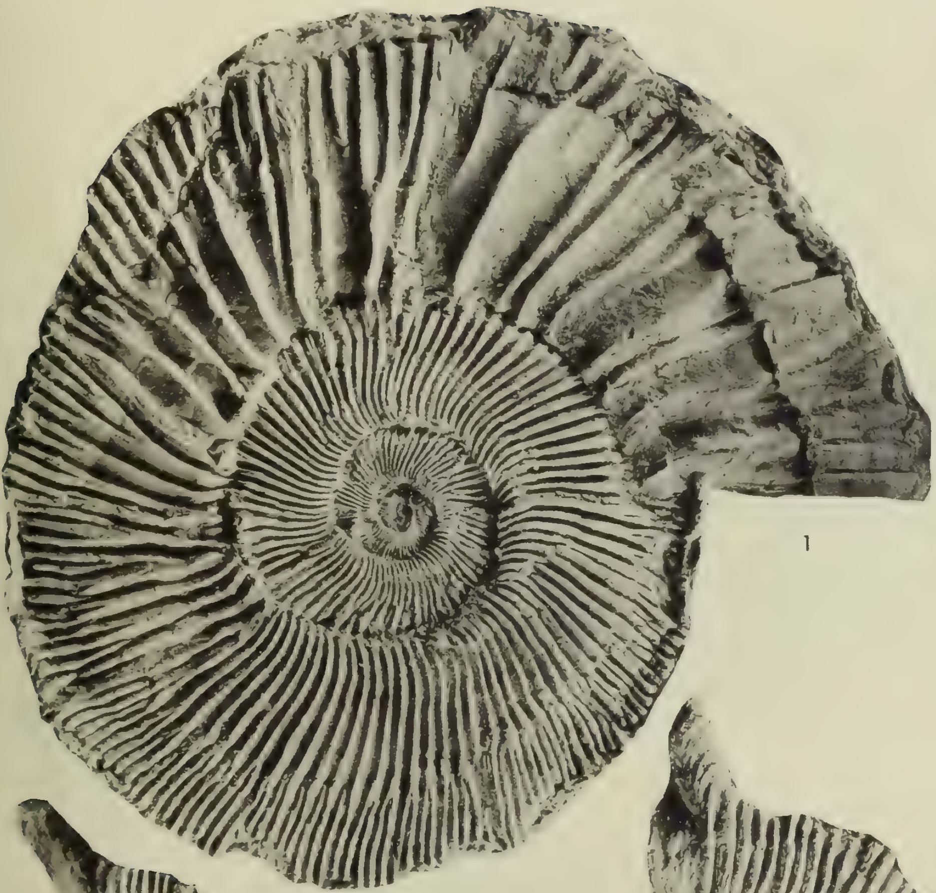


PLATE 23

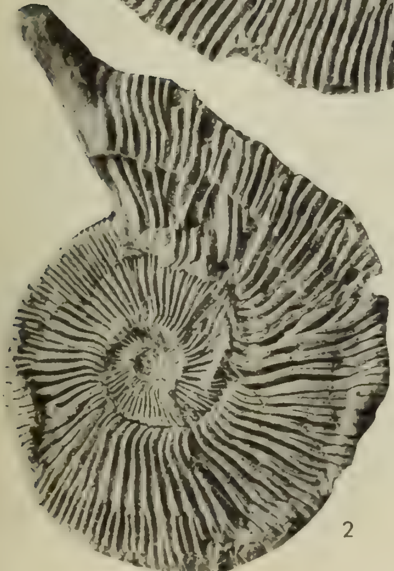
Fig. 1. ***Pectinatites (Virgatosphinctoides) reisiformis densicostatus*** subsp. nov. Holotype (macroconch), C.73437, ×0·85, 13 feet above Rope Lake Head Stone Band.

Fig. 2. ***Pectinatites (Virgatosphinctoides) reisiformis densicostatus*** subsp. nov. Paratype (microconch), C.73438, ×0·85, 13 feet above Rope Lake Head Stone Band.

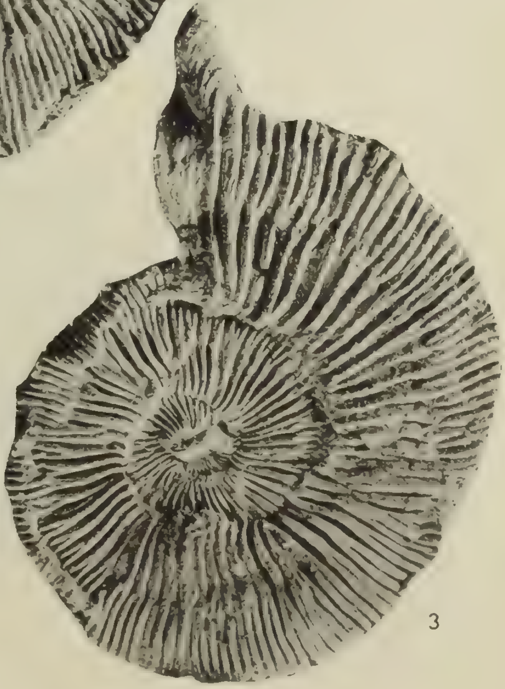
Fig. 3. ***Pectinatites (Virgatosphinctoides) reisiformis*** sp. nov. Paratype (microconch), C.73436, ×0·85, 13 feet above Rope Lake Head Stone Band.



1



2

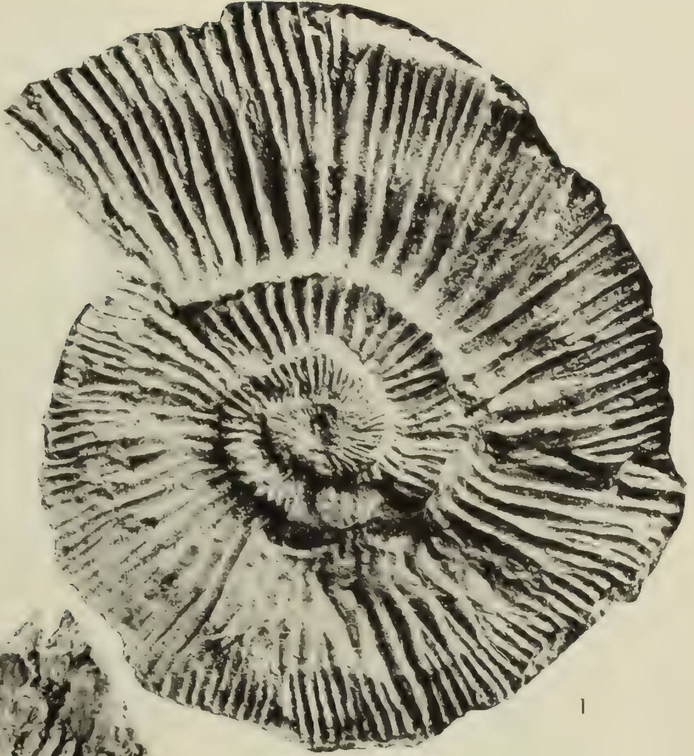


3

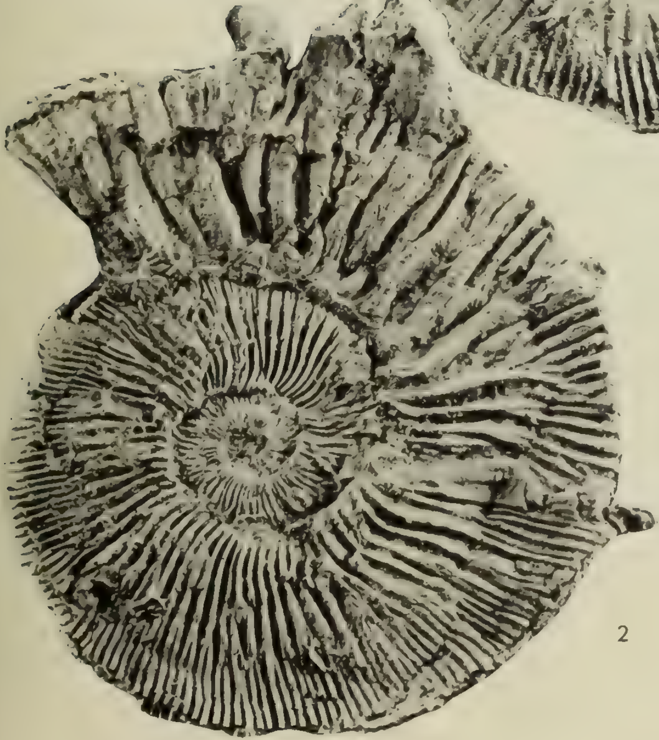
PLATE 24

FIG. 1. ***Pectinatites* (*Virgatosphinctoides*) *wheatleyensis minor*** subsp. nov. Holotype (macroconch), C.73429, ×0·85, 17 feet below Blackstone.

FIG. 2. ***Pectinatites* (*Virgatosphinctoides*) *reisiformis densicostatus*** subsp. nov. Intersex, C.73439, ×0·85, 13 feet above Rope Lake Head Stone Band.



1



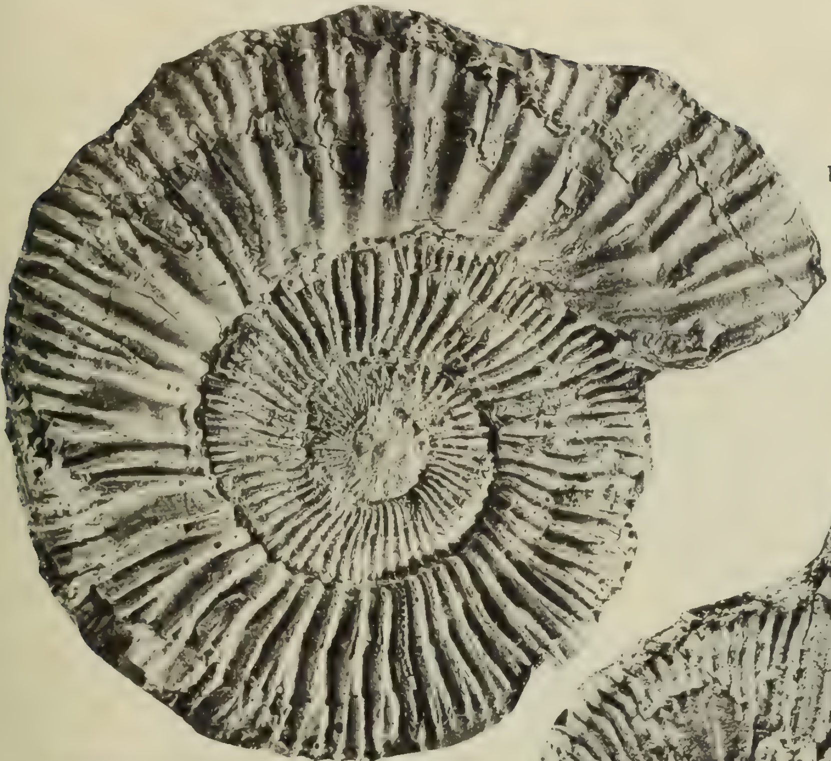
2

PLATE 25

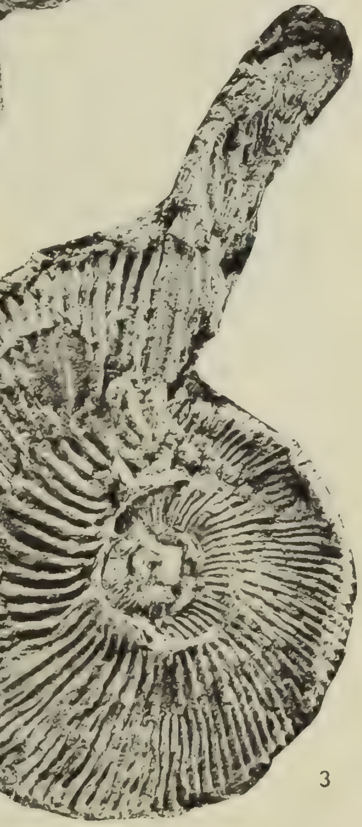
FIG. 1. ***Pectinatites* (*Virgatosphinctoides*) *donovani*** sp. nov. Holotype (macroconch), C.73441, ×0·85, 30 feet below Basalt Stone Band.

FIG. 2. ***Pectinatites* (*Virgatosphinctoides*) *donovani*** sp. nov. Paratype (microconch), C.73442, ×0·85, 36 feet below Basalt Stone Band.

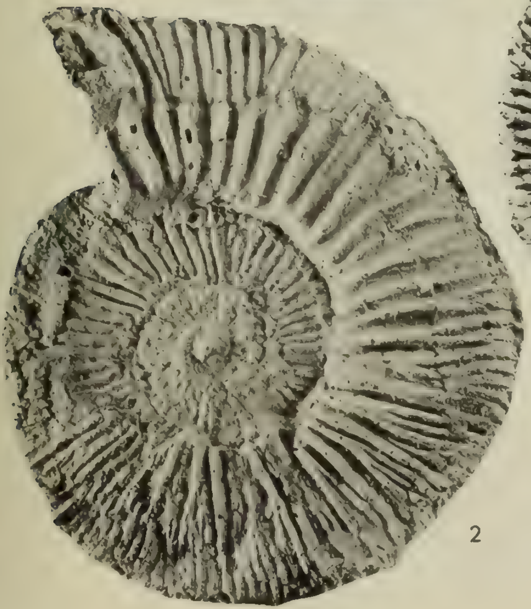
FIG. 3. ***Pectinatites* (*Pectinatites*) *cornutifer*** (Buckman). Microconch, C.73451, ×1, 6 feet above Freshwater Steps Stone Band.



1



3



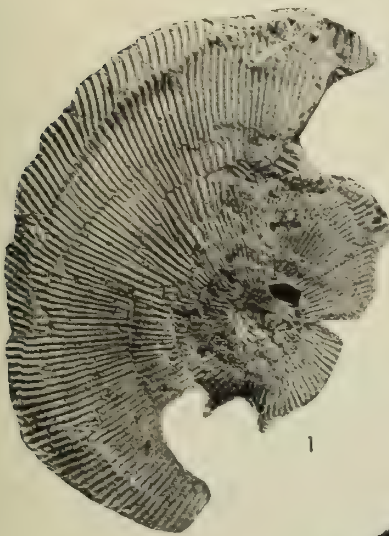
2

PLATE 26

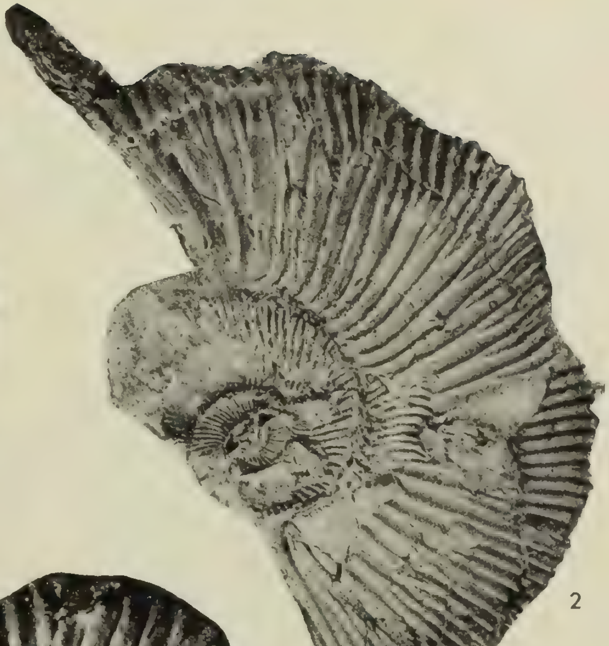
FIG. 1. ***Pectinatites* (*Pectinatites*) *eastlecottensis*** (Salfeld). Microconch, C.73449, × 1, 10 feet above Middle White Stone Band.

FIG. 2. ***Pectinatites* (*Pectinatites*) *cornutifer*** (Buckman). Microconch, C.73450, × 1, 6 feet below Freshwater Steps Stone Band.

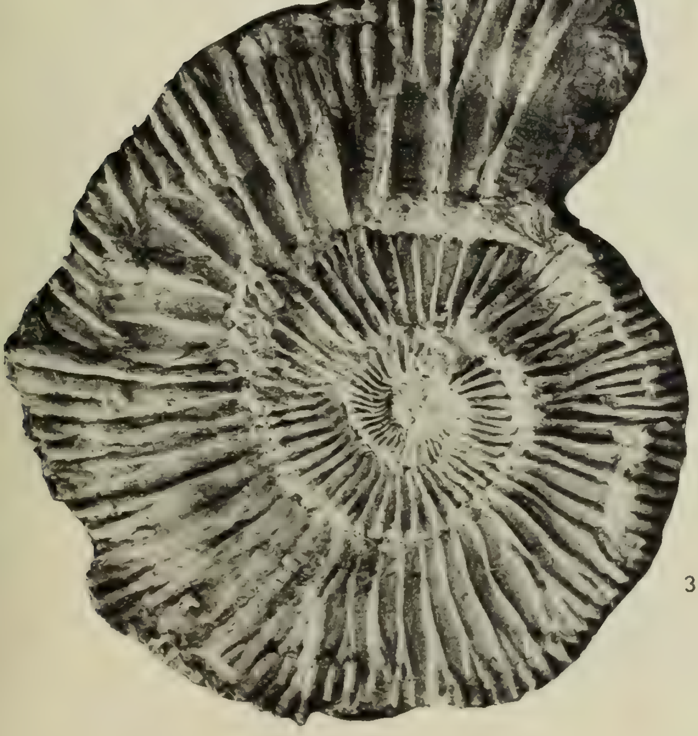
FIG. 3. ***Pectinatites* (*Virgatosphinctoides*) *abbreviatus*** sp. nov. Holotype (macroconch), C.73440, × 1, 20 feet above Rope Lake Head Stone Band.



1



2



3

PLATE 27

Fig. 1. ***Pectinatites (Virgatosphinctoides) encombensis*** sp. nov. Holotype (microconch), C.73444, × 1, 21 feet below White Stone Band.

Fig. 2. ***Pectinatites (Virgatosphinctoides) wheatleyensis delicatulus*** (Neaverson). Macroconch, C.73428, × 1, 4 feet below Blackstone.

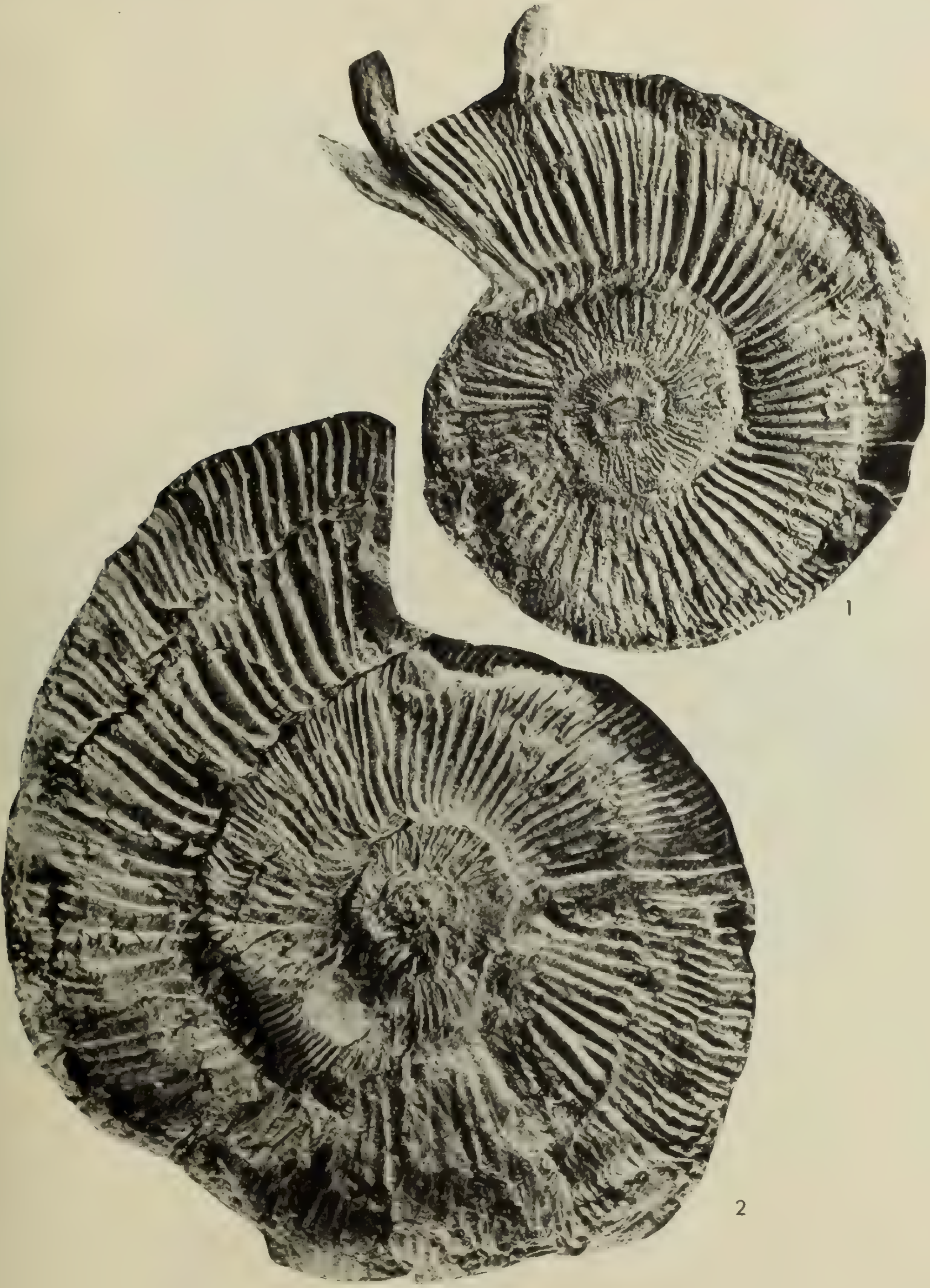

1
2

PLATE 28

Pectinatites* (*Virgatosphinctoides*) *encombensis sp. nov. Paratype (macroconch), C.73445, ×0·75, 33 feet below White Stone Band.

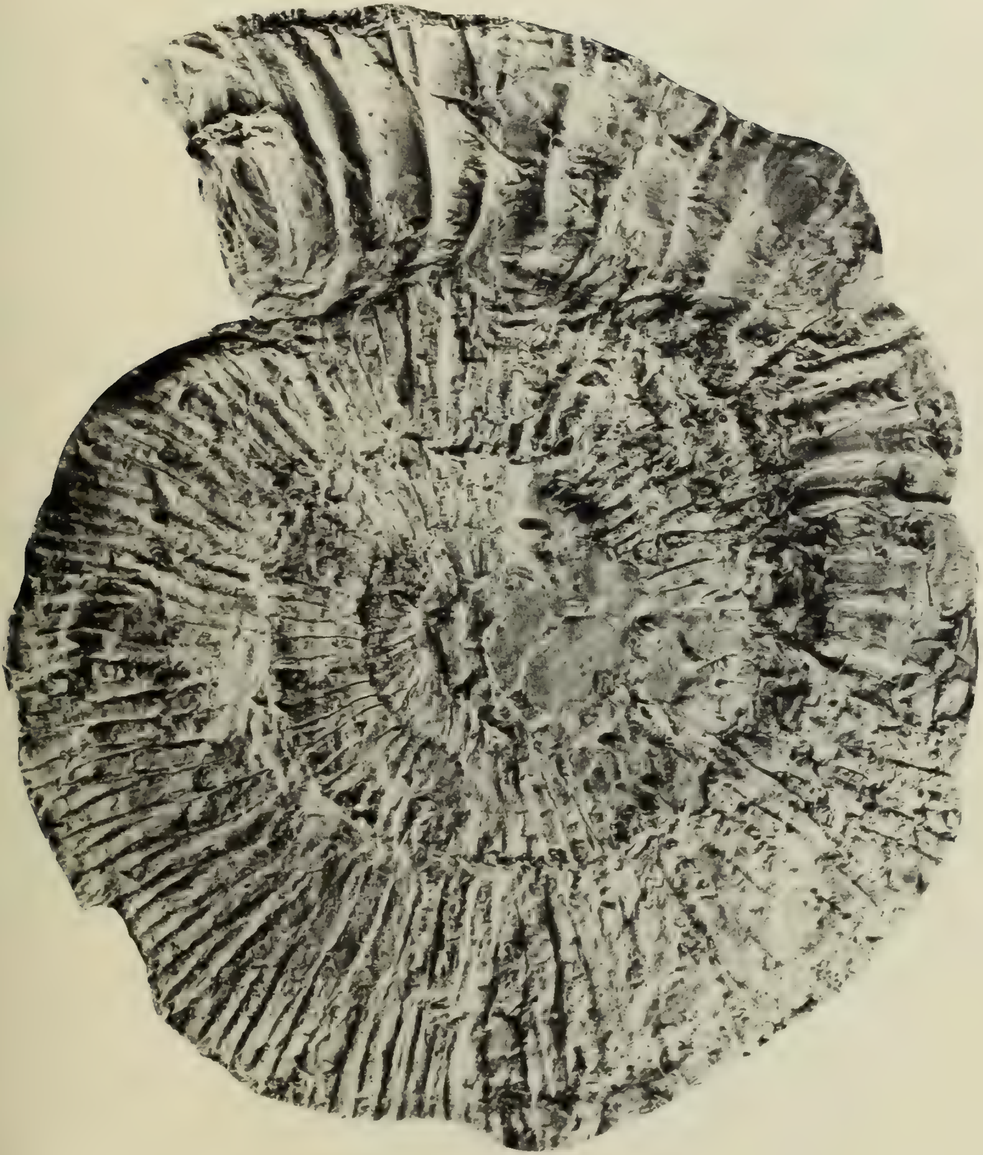


PLATE 29

Pectinatites* (*Virgatosphinctoides*) *magnimasculus sp. nov. Holotype (microconch), C.73443, × 1, 21 feet below White Stone Band. The postulated rib density of missing parts of the shell indicated by broken lines.

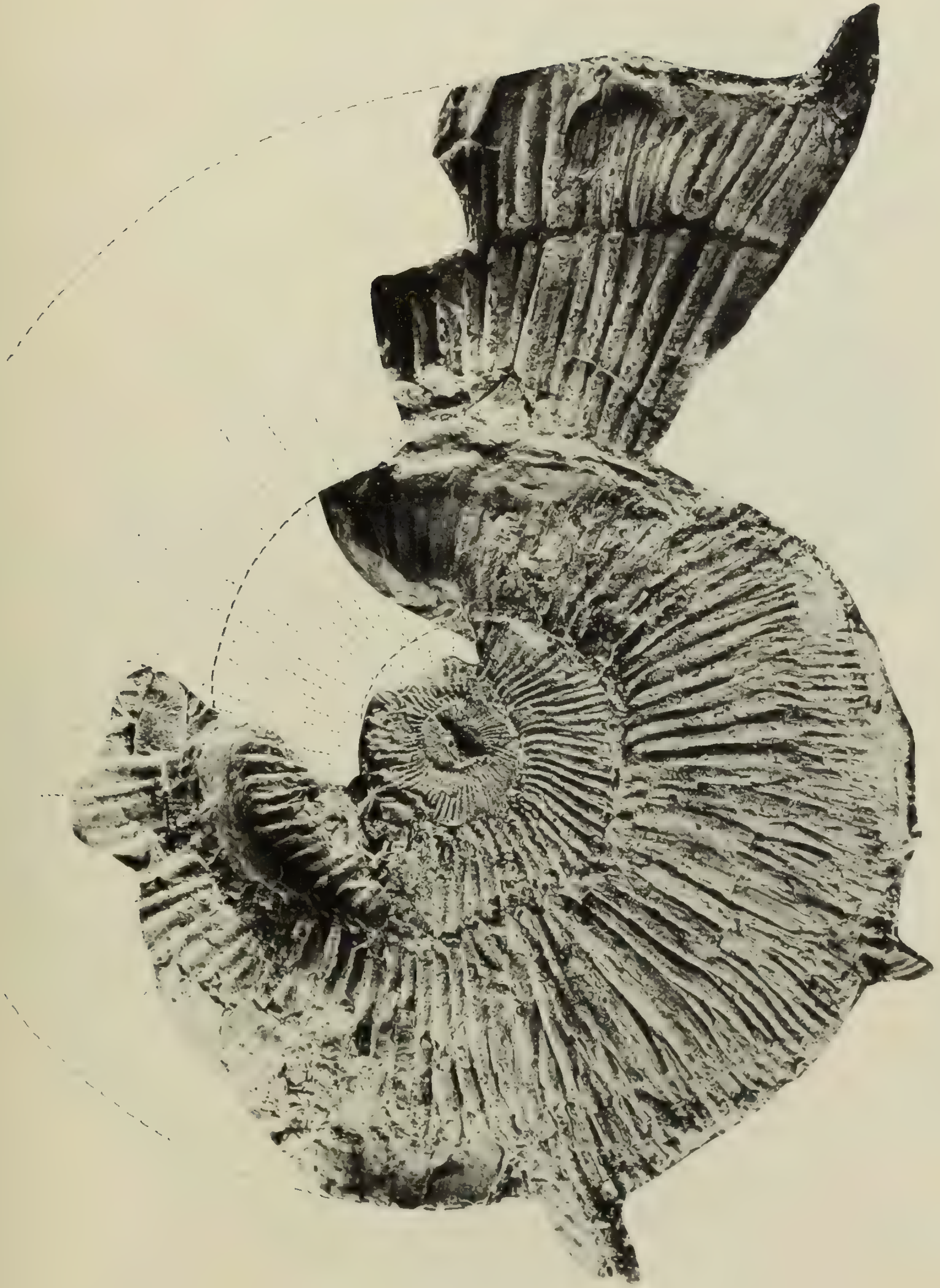
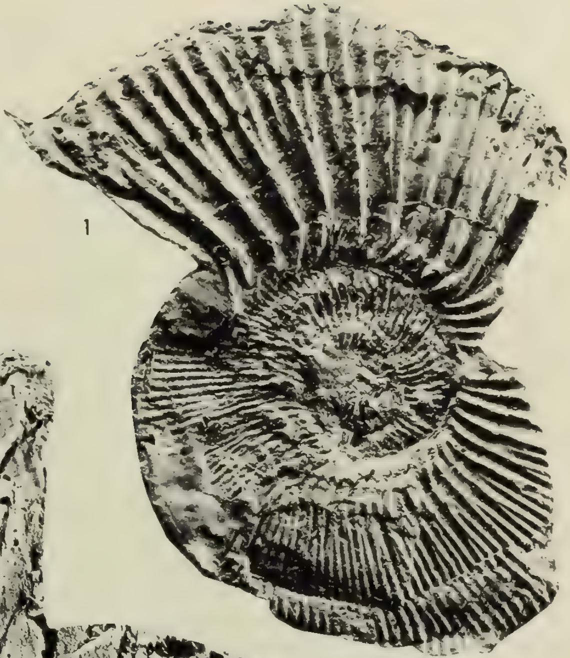


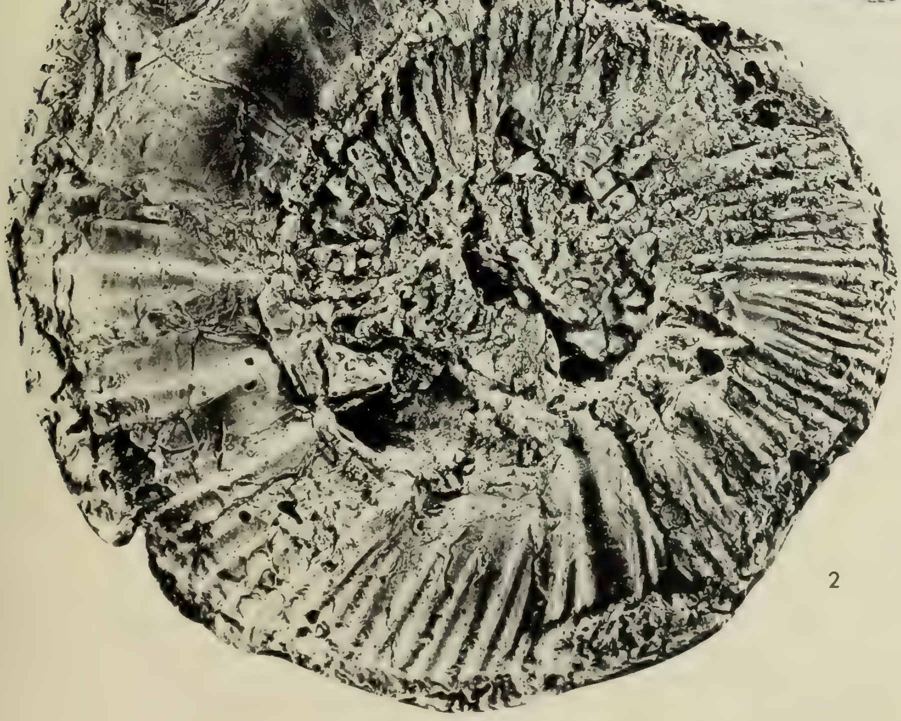
PLATE 30

Fig. 1. ***Pectinatites* (*Pectinatites*) *inconsuetus*** sp. nov. Paratype (micrconch), C.73447, ×1, 10 feet above Middle White Stone Band.

Fig. 2. ***Pectinatites* (*Pectinatites*) *inconsuetus*** sp. nov. Holotype (macroconch), C.73446, ×0·9, 10 feet above Middle White Stone Band.



1



2

PLATE 31

Pectinatites (Pectinatites) groenlandicus (Spath). Macroconch, C.73448, ×0·5, 10 feet above Middle White Stone Band.

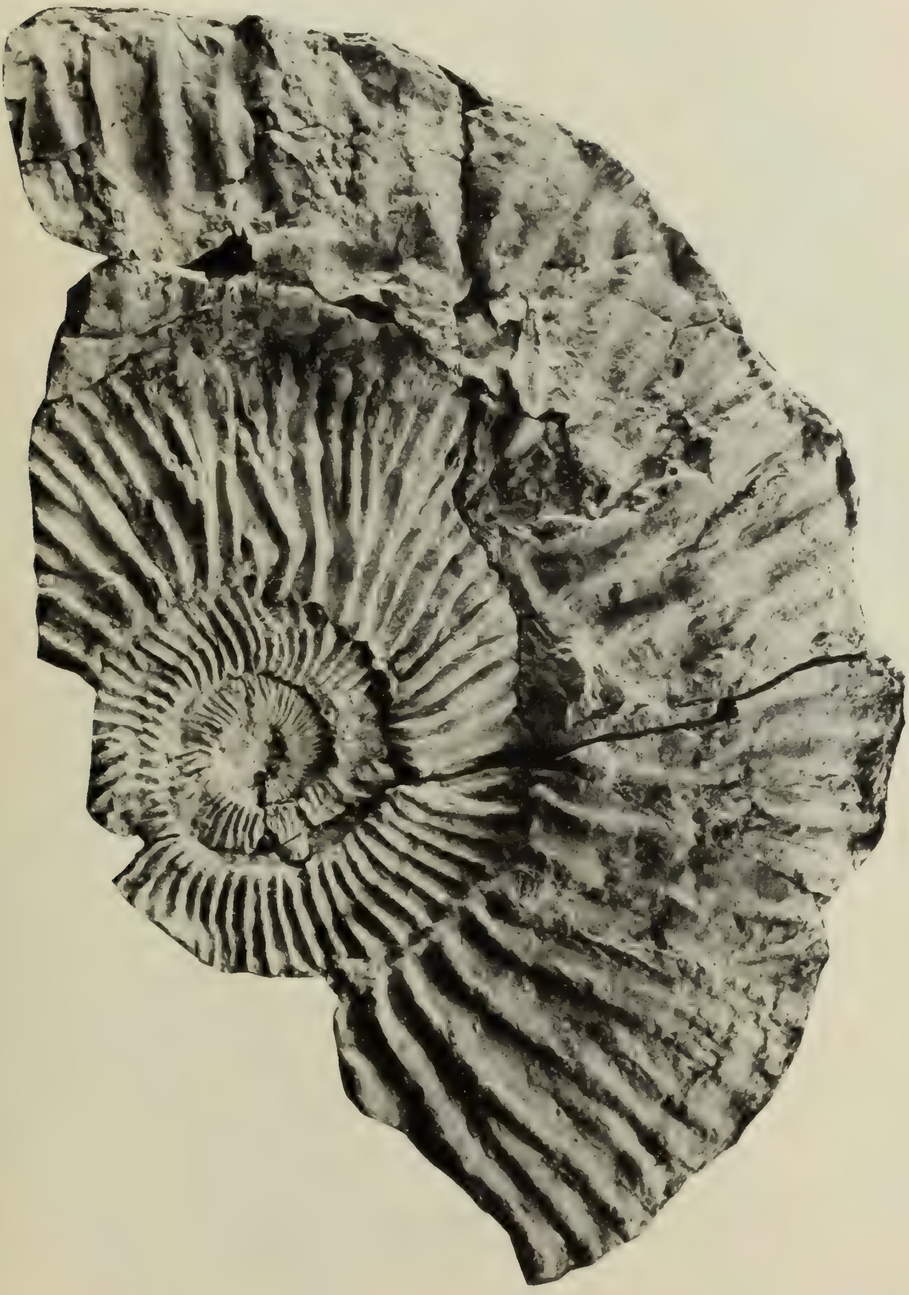
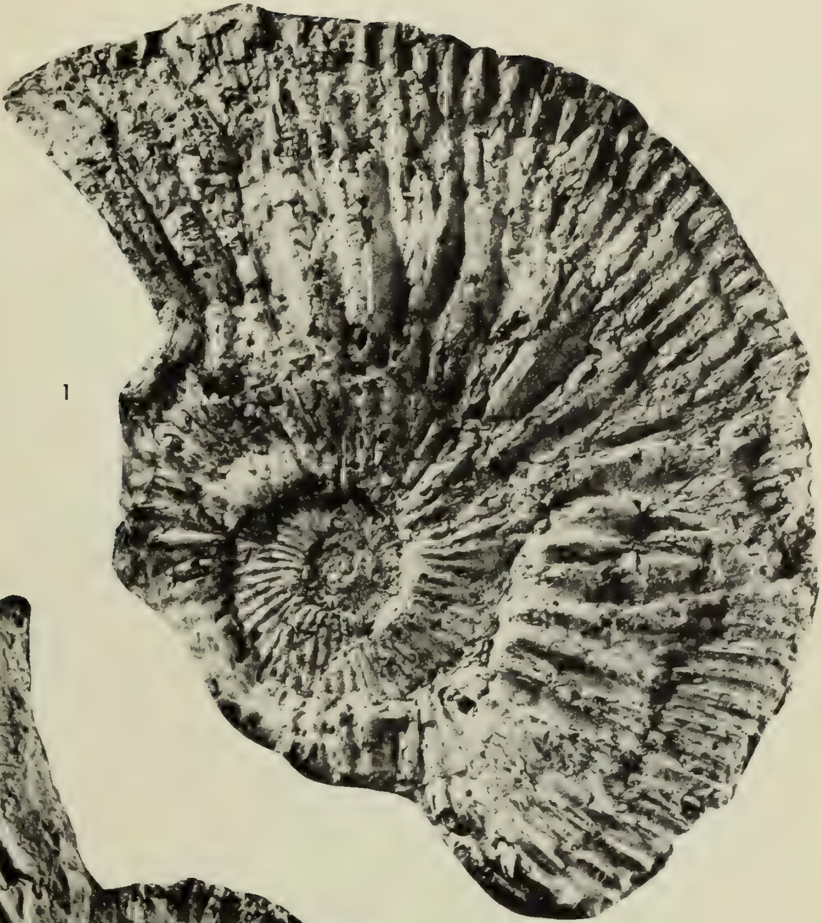


PLATE 32

Fig. 1. ***Pectinatites (Pectinatites) naso*** (Buckman). Macroconch, C.73452, × 1, 10 feet above Freshwater Steps Stone Band.

Fig. 2. ***Pectinatites (Pectinatites) naso*** (Buckman). Microconch, C.73453, × 1, 10 feet above Rope Lake Head Stone Band.

1



2

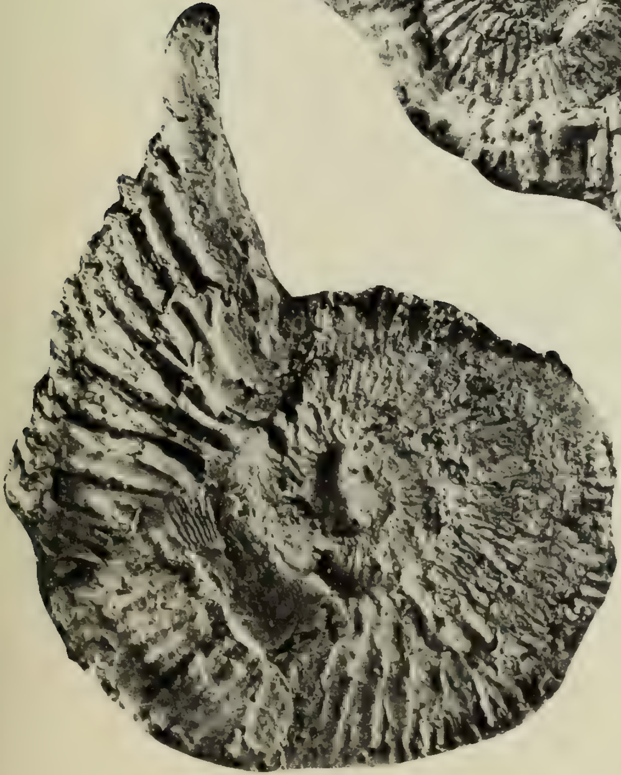
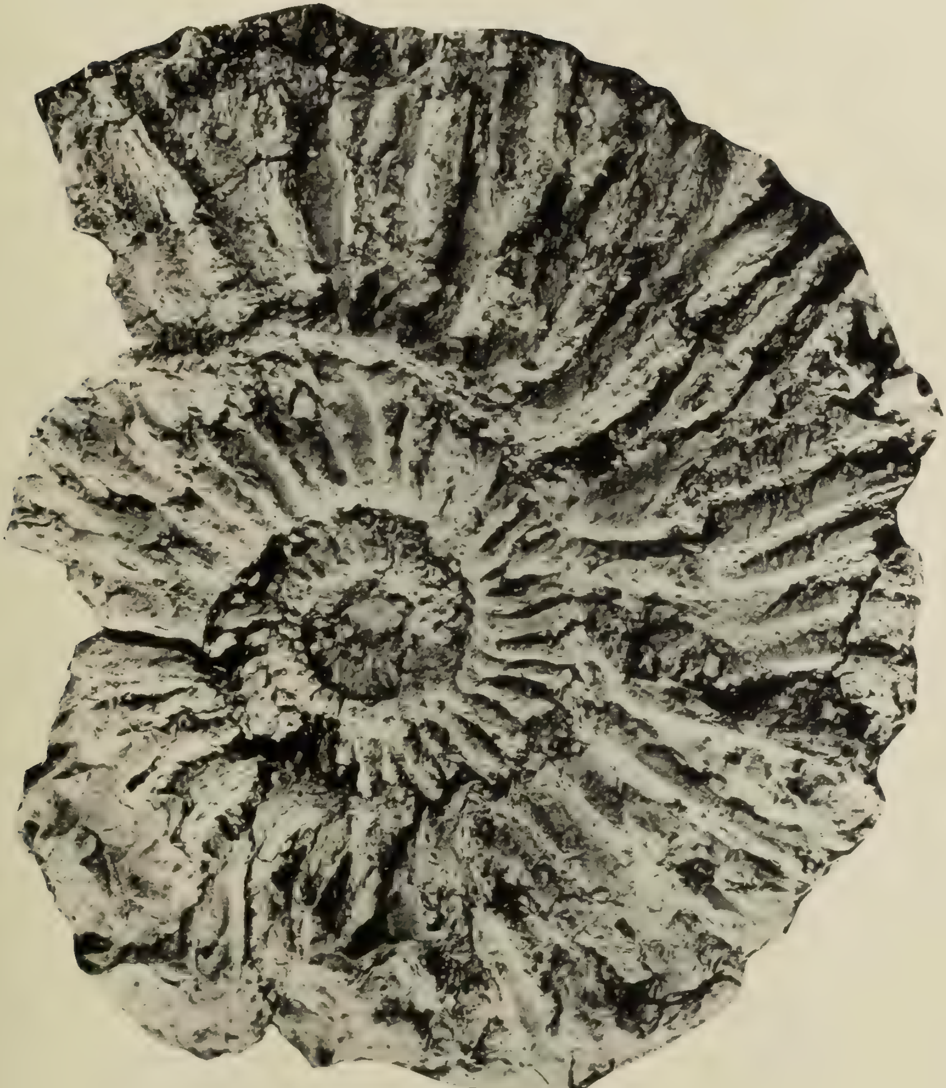


PLATE 33

Pavlovia* (*Paravirgatites*)** cf. ***paravirgatus (Buckman). C.73454, × 1·1, 10 feet above Freshwater Steps Stone Band.



BRITISH MUSEUM
25 MAY 1967
NATURAL HISTORY

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

12 JUN
NATURAL HIST

THE CORRELATION AND TRILOBITE FAUNA OF THE BEDINAN FORMATION (ORDOVICIAN) IN SOUTH-EASTERN TURKEY

W. T. DEAN

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 2
LONDON: 1967

12 JU
NATURAL

THE CORRELATION AND TRILOBITE FAUNA OF THE BEDINAN FORMATION (ORDOVICIAN) IN SOUTH-EASTERN TURKEY

BY

WILLIAM THORNTON DEAN, D.Sc.

Pp. 81–123 ; 10 *Plates* ; 4 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 2
LONDON : 1967

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 15, *No.* 2 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation:
Bull. Br. Mus. nat. Hist. (Geol.).

© Trustees of the British Museum (Natural History) 1967

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 13 *June*, 1967 *Price* £2

THE CORRELATION AND TRILOBITE FAUNA OF THE BEDINAN FORMATION (ORDOVICIAN) IN SOUTH-EASTERN TURKEY

By W. T. DEAN

MS accepted November, 30, 1966

CONTENTS

		Page
I.	INTRODUCTION AND ACKNOWLEDGMENTS	84
II.	THE SUCCESSION AT BEDINAN	85
III.	THE SUCCESSION NEAR SOSINK	89
IV.	AGE AND RELATIONSHIPS OF THE BEDINAN FAUNAS	91
V.	SYSTEMATIC DESCRIPTIONS	93
	Ampyx nitidus sp. nov.	93
	Marrolithoides orthogonius sp. nov.	96
	Marrolithoides laticirrus sp. nov.	99
	Cryptolithus? inferus sp. nov.	102
	Cryptolithus? bedinanensis sp. nov.	104
	Dionide formosa (Barrande) *anatolica* subsp. nov.	109
	Dalmanitina proaeva proaeva (Emmrich)	112
	Kloucekia phillipsii (Barrande) *euroa* subsp. nov.	113
	Cheirurid gen. et sp. indet.	114
	Neseuretus (*Neseuretinus*) *turcicus* subgen. et sp. nov.	115
	Brongniartella levis sp. nov.	118
	Platycoryphe? sp.	120
	Colpocoryphe sp.	120
	Selenopeltis inermis (Beyrich) *angusticeps* subsp. nov.	121
	Asaphid gen. et sp. indet.	121
VI.	REFERENCES	122

SYNOPSIS

The strata of the Bedinan Formation are described from the type region between Derik and Mardin, south-eastern Turkey. The rocks, which rest unconformably upon the Sosink Formation (Cambrian), are mostly mudstones and shales but the highest of these pass upwards, apparently without a break, into a group of sandstones. The Bedinan Formation represents only a part of the Caradoc Series and there is an abundant shelly fauna which includes the following trilobites: *Ampyx nitidus* sp. nov., *Marrolithoides orthogonius* sp. nov., *M. laticirrus* sp. nov., *Cryptolithus? inferus* sp. nov., *C? bedinanensis* sp. nov., *Dionide formosa anatolica* subsp. nov., *Dalmanitina proaeva* (Emmrich), *Kloucekia phillipsii euroa* subsp. nov., *Neseuretus* (*Neseuretinus*) *turcicus* subgen. et sp. nov., *Brongniartella levis* sp. nov., *Platycoryphe?* sp., *Colpocoryphe* sp., *Selenopeltis inermis angusticeps* subsp. nov. The trilobites, together with the less common brachiopods, exhibit marked Bohemian/Tethyan affinities and a tentative correlation with the Černín and Chlustina Beds of Czechoslovakia is suggested. The graptolite evidence, though fragmentary, probably indicates the *multidens* or *clingani* Zone and is broadly in keeping with that of the shelly faunas.

I. INTRODUCTION AND ACKNOWLEDGMENTS

Although large outcrops of Lower Palaeozoic rocks occur in south-eastern Turkey, between the Tigris and Euphrates valleys, relatively little published information is available. The best-known exposures lie along an elongated belt, up to almost 3 km. wide, running east-south-east from a point 2 km. south-east of Derik towards Mardin, about 20 km. north-west of the Syrian frontier (for place names see Text-fig. 1). Tolun & Ternek (1952) gave a short description and small-scale maps of the Cambrian outcrops near Derik, and the highest part of the Cambrian succession as shown by them is known now to be Ordovician in age. Later Tolun (1960 : 236) noted the occurrence of Silurian rocks (*sensu lato* including Ordovician) in south-eastern Turkey and mentioned a succession of 900 m. of marly and sandy beds with brachiopods, graptolites and trilobites underlying Cretaceous limestones at Bedinan. He remarked also on the similarity of the Bedinan Ordovician rocks to others found in bore-holes in northern Syria. The most important work dealing with this region is that of Kellogg (1960) who mapped a large area west of Mardin and gave detailed sections through all the stratigraphical subdivisions present, including the Cambrian and Ordovician rocks. He gave no comprehensive faunal lists but described the Bedinan Formation as containing, especially, " *Cryptolithus* " and " *Sowerbyella*-like brachiopods ", which were held to indicate a Middle Ordovician age. Unfortunately Kellogg's report remains unpublished, but reference will be made to his work from time to time in this paper. A chart of the rock succession in south-eastern Turkey, from Pre-Cambrian to Quaternary, was compiled by Gernot Schmidt

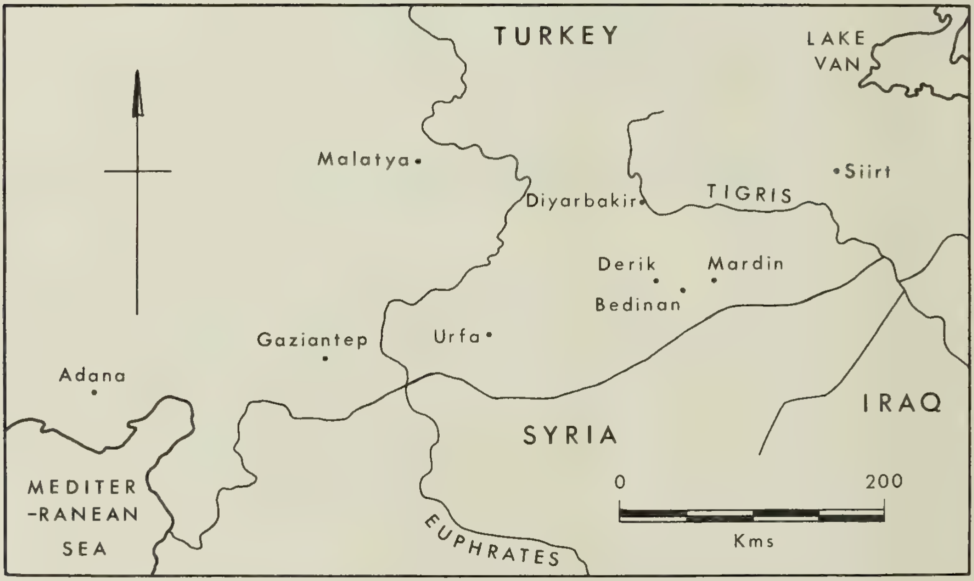


Fig. 1. Sketch-map of south-eastern Turkey showing location of place-names mentioned in text.

in 1964 and revised in 1965. Again, this is a publication that I have been unable to find generally available, though some of its conclusions are noted later.

During the Spring of 1965 my wife and I carried out field-work in the region between Derik and Mardin. Both the Cambrian and Ordovician successions were examined ; the latter are now described and it is proposed to describe the Cambrian faunas at a later date. Our work was greatly facilitated by the kindness of numerous Turkish friends. The Director, Dr. Sadrettin Alpan, and other members of the Maden Tetkik ve Arama Enstitüsü (M.T.A.), Ankara, generously placed the facilities of their organization at our disposal and we are particularly indebted to Dr. and Mrs. Kıraglı, as well as to Mr. Günal Aygün who helped us in the field. In the Derik region we received much help from Dr. Karaköyunlu and members of the M.T.A. base-camp at the Mazıdag, whilst the work of Mr. Abdurrahman Tunç as guide and collector was invaluable. While working on comparative material in Czechoslovakia we received kindly assistance from Dr. Radvan Horný and Dr. Ladislav Marek. The graptolites we collected were examined by Dr. Isles Strachan. Finally, Prof. H. B. Whittington read the manuscript and made suggestions for its improvement. All specimens described in the present work are in the collections of the Department of Palaeontology, British Museum (Natural History).

II. THE SUCCESSION AT BEDINAN

The village of Bedinan (sometimes written as Badinan or Bahdinan) lies in a valley about 20 km. east-south-east of Derik. The Ordovician rocks there form an inlier about 6 km. long and up to 3 km. broad elongated in an east-west direction. The inlier is bounded to the north by a prominent scarp and plateau of unconformable Cretaceous limestones, with a gentle northerly dip, and to the south by a large east-west dislocation, the Mardin Fault, which delimits massive Tertiary limestones having a variable southerly dip and sometimes slightly overturned. For the most part the Ordovician rocks comprise mudstones and shales with some intercalations of calcareous siltstone ; the latter sometimes exhibit cone-in-cone structure and are more resistant to erosion than the adjacent mudstones. Higher in the succession the beds become more arenaceous and pass upwards conformably into a series of current-bedded sandstones, the age of which is discussed later.

The principal section of the Bedinan Formation occurs to the west of the village. The succession there is almost totally argillaceous, broken only by occasional, sometimes concretionary, bands of siltstone. The strata have a slightly variable dip of rather more or less than 40° to the north-north-east, and by means of a traverse in this direction it was possible to sample the rocks in ascending order. The location and horizons of the principal fossiliferous localities are shown in Text-figs. 2 and 3. The lowest beds presumably occurring here form a low-lying area immediately adjacent to hills of more resistant Tertiary limestones, and could not be examined owing to the cover of Alluvium. Consequently it was impossible to confirm the suggestion, made elsewhere in this paper, that these lowest strata may probably be correlated, at least in part, with the relatively restricted Ordovician succession of the Sosink district. However, the lowest beds sampled (at localities B.1 and B.2) yielded *Neseuretus* (*Neseuretinus*) *turcicus* sp. nov., *Colpocoryphe* sp., *Ampyx*

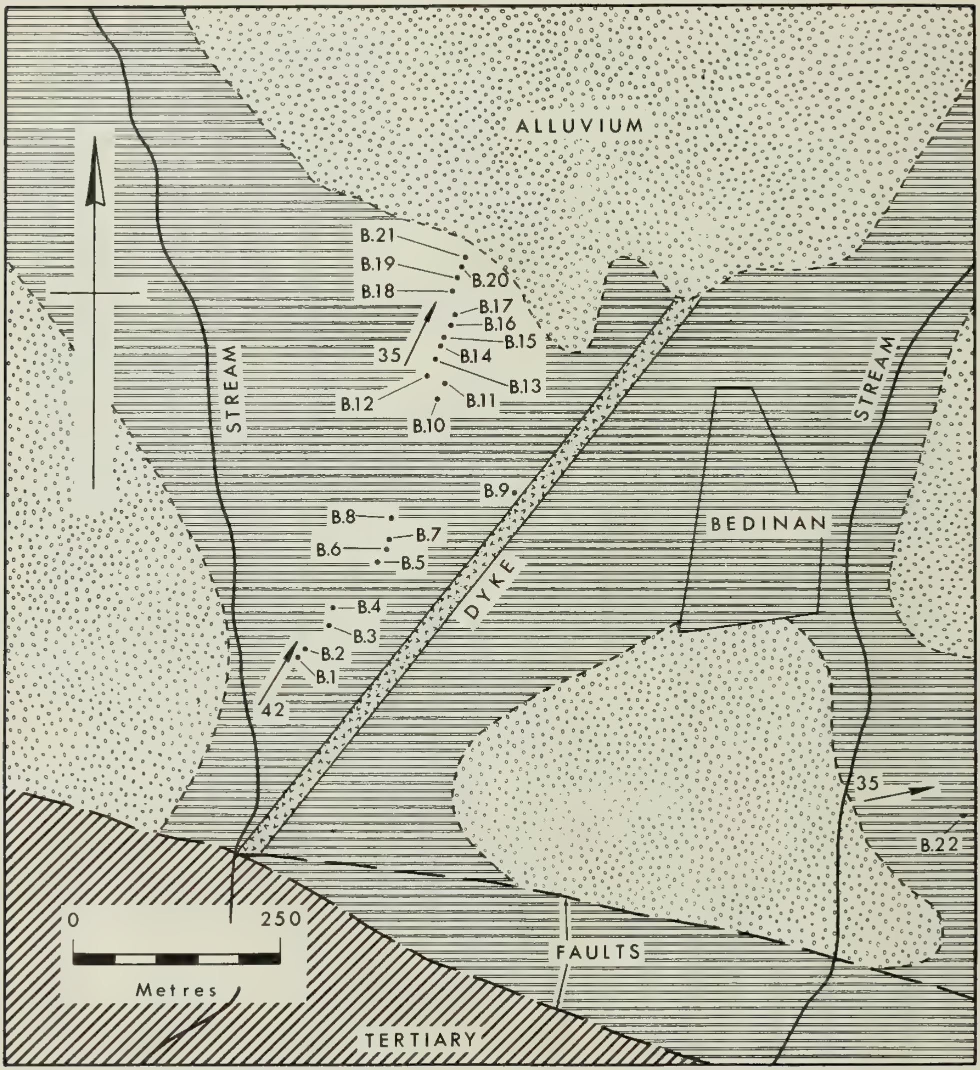

ALLUVIUM
B.21
B.19
B.20
B.18
B.17
B.16
B.15
35
B.14
B.13
B.12
B.11
B.10
STREAM
STREAM
B.9
BEDINAN
B.8
B.7
B.6
B.5
DYKE
B.4
B.3
B.2
B.1
42
35
B.22
0
250
Metres
FAULTS
TERTIARY

Fig. 2. Sketch-map showing principal fossil localities in the Ordovician rocks (horizontal shading) near Bedinan. Diagonal shading denotes Tertiary strata, whilst the remaining areas are covered by Alluvium.

nitidus sp. nov., *Cryptolithus*? and *Selenopeltis inermis angusticeps* ssp. nov. Three of these genera are known from near Sosink but were not recorded from the succeeding strata near Bedinan. *Dalmanitina* and *Kloucekia* did not prove suitable for attempts to subdivide the Bedinan Formation, and were found to persist, virtually unchanged, throughout.

Perhaps the least fossiliferous group of strata encountered in the traverse were those in the middle part of the section, including localities B.5–B.9. Nevertheless, sufficient material was collected to show that the fauna differs in no way from that of the higher beds. The strata in this and lower parts of the succession were disturbed by the intrusion of a dyke alleged by Kellogg (1960) to be of Quaternary age. The adjacent shales are often broken and collecting there is difficult, but the degree of metamorphism is not high and at one point, near locality B.9, relatively undistorted fossils were obtained within a few centimetres of the contact.

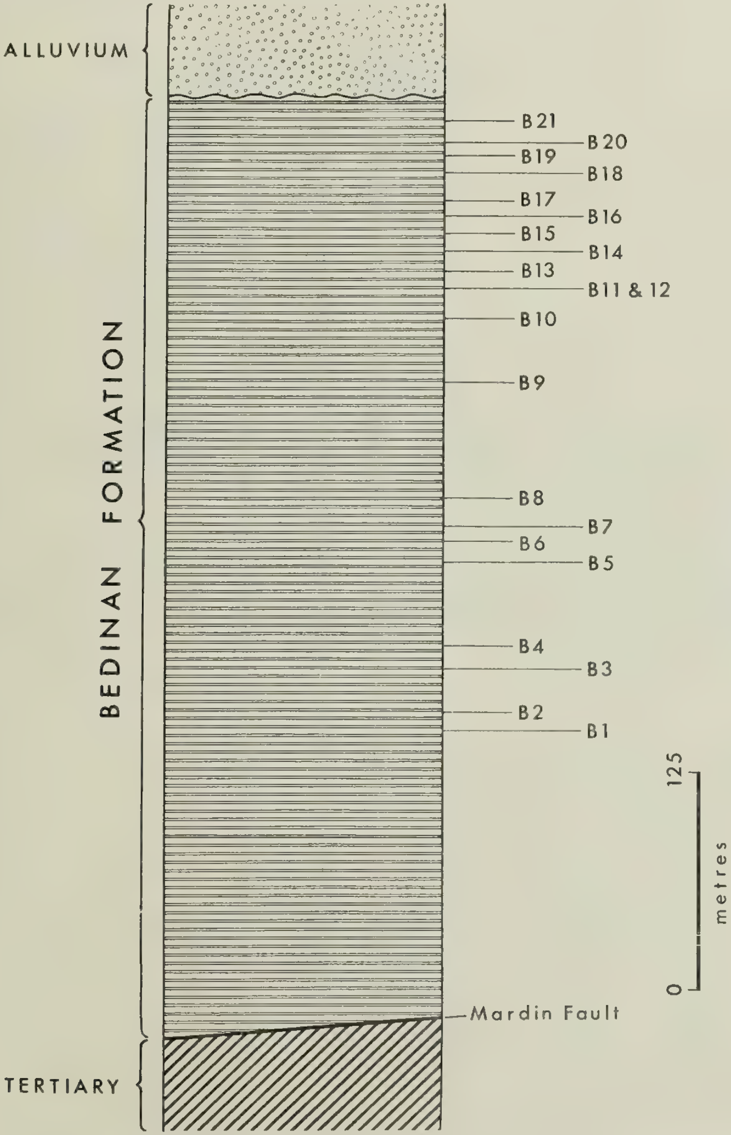

ALLUVIUM
BEDINAN FORMATION
TERTIARY
B21
B20
B19
B18
B17
B16
B15
B14
B13
B11 & 12
B10
B9
B8
B7
B6
B5
B4
B3
B2
B1
Mardin Fault
125
metres
0

FIG. 3. Diagrammatic vertical section of the strata just west of Bedinan, showing horizons of principal Ordovician fossil localities. Shading as in Text-fig. 2.

The highest group of strata exposed in this section crop out along a hill-slope capped by superficial deposits. The beds mostly comprise grey-green shales which weather yellowish-brown and crumble easily. They are sometimes highly fossiliferous, containing especially trinucleid trilobites (*Cryptolithus*?), *Dalmanitina* and *Kloucekia*; the specimens are often compressed, but occasional micaceous siltstone bands may yield less distorted material. Brachiopods, including the genera *Aegiromena* and *Svobodaina*, of Bohemian affinities, were found at several localities but proved particularly abundant at B.18–B.21.

According to Kellogg, still higher strata near Bedinan may be examined in the area to the south-east of the village, and a traverse was made in that direction. His measured section shows the shale succession passing upwards into a thick series of sandstones, the age of which he put at " Middle? or Upper? Ordovician ", these being followed in turn by unfossiliferous sandstones and shales of the Dadaș Formation, of " Lower? Silurian " age. More recently Schmidt (1965) has assigned the Bedinan Formation to both the Ordovician and the Silurian, followed (though the nature of the contact is questionable) by the Dadaş Formation, of alleged Devonian age. Whatever the relative merits of these two schemes, and there is as yet no definite faunal evidence to support either, it seems clear that the shales and mudstones forming the bulk of the Bedinan Formation pass upwards conformably into a series of massive and flaggy, often current-bedded sandstones. The higher, more massive, arenaceous strata yielded no more than occasional indeterminate fragments of inarticulate brachiopods, but in the lower sandstones I was able to find occasional specimens of *Dalmanitina* and *Kloucekia*, apparently identical with the forms occurring so abundantly in the argillaceous strata near Bedinan. As discussed elsewhere in this paper, the faunas of the argillaceous Bedinan Formation suggest an horizon in the upper half, though not the highest part, of the Caradoc Series. Consequently there is no necessity to regard at least the lower portion of the succeeding sandstone sequence as being any later than Caradoc in age.

FAUNAL LIST (for localities see Text-fig. 2)

Ampyx nitidus sp. nov. B.2.
Brongniartella levis sp. nov. B.18.
Brongniartella sp. B.13, 19, 20.
Cheirurid gen. et sp. indet. B.12.
Colpocoryphe sp. B.1, 2.
Dalmanitina proaeva proaeva (Emmrich) B.1–3, 6, 7, 10, 11, 13–15, 17–22.
Kloucekia phillipsii (Barrande) *euroa* subsp. nov. B.2–4, 6–8, 11–21.
Cryptolithus? *inferus* sp. nov. B.1.
Cryptolithus? cf. *inferus* sp. nov. B.2, 3.
Cryptolithus? *bedinanensis* sp. nov. B.6, 8–16, 20, 22.
Marrolithoides laticirrus sp. nov. B.3, 4.
Marrolithoides sp. B.18? B.21.
Neseuretus (*Neseuretinus*) *turcicus* subgen. et sp. nov. B.2.
Platycoryphe ? sp. B.20.

Selenopeltis inermis (Beyrich) *angusticeps* subsp. nov. B.1.
Ostracoda indet. B.8, 17, 22.
Aegiromena sp. B.1–3, 6, 8, 9.
Lingula sp. B.7.
Schizocrania sp. B.1.
Svobodaina sp. B.2, 6, 8, 10–12, 17–21.
Trematis? sp. B.13.
Ribeiria sp. B.3.
Miscellaneous, poorly-preserved bivalves B.1–3, 6–8, 16.
Sinuites (s.l.) sp. B.3.
Hyolithids indet. B.10.
Lepidocoleus sp.
Plumulites sp. B.10, 12, 13, 16, 22.
Crinoid fragments, B.13, 20.
Climacograptus sp. B.13.
Diplograptus sp. B.8.

III. THE SUCCESSION NEAR SOSINK

Although the Bedinan Formation forms an elongated E-W outcrop some 5 km. by 1 km. just east of the village of Sosink, the strata are not well exposed. Much of the ground is covered by superficial deposits derived from the adjacent high ground to the east where Cretaceous limestones, dipping south, form a plateau-like unconformable layer, and the best exposures are limited to a section running N.N.W.–S.S.E. along the dip, in the vicinity of the small stone building known as Ziyaret (Text-fig. 4). The rocks, like those of the Bedinan district, consist essentially of grey-green mudstones and shales with occasional, harder bands of siltstone. The beds dip just east of south at an average angle of about 38° though with slight variations, and the estimated thickness, calculated on the basis of a section through Ziyaret, is of the order of 440 m. In general the rocks are poorly fossiliferous, though specimens may be locally abundant, occurring in thin bands. The mudstones and shales are deeply weathered and crumble easily whilst the fossils are almost invariably preserved as orange, limonitic, internal and external moulds.

The northern boundary of the Ordovician outcrop here is a fault, separating the beds from Cambrian sandstones which form a conspicuous feature immediately to the north. The fault has an indeterminate, small downthrow to the south and is thought to mask the unconformable base of the Bedinan Formation. The lowest Ordovician beds exposed are not far from the fault-line and proved only sparingly fossiliferous, locality A.1 yielding a single specimen of *Colpocoryphe* and a few poorly-preserved brachiopods. Much of the Ordovician succession exposed in the hill-slopes to the south-east of Ziyaret proved almost barren, and only a small number of specimens was obtained from locality A.2 though these did include *Lasiograptus* sp. and the holotype cranidium of *Selenopeltis inermis angusticeps* subsp. nov. in addition to the more commonplace fauna of *Dalmanitina*, *Aegiromena* and bellerophontid gastropods (*Sinuites* s.l.).

The most prolific faunas of this area were collected from a number of localities in a small N.E.–S.W. valley excavated in shales some 180 m. north-west of the estimated position of the Cretaceous/Ordovician unconformity. In general the fossils were found in restricted horizons, no more than a few cm. thick, which could not be traced with certainty for more than a few metres. Trinucleid trilobites (*Marrolithoides*) formed easily the most abundant constituent of the fauna, though *Dalmanitina* and *Kloucekia* were not uncommon. The presence of *Dionide formosa anatolica* at three localities was of particular interest ; the species was found within a thickness of only a few metres of shales, and the genus is not yet known elsewhere in south-eastern Turkey. Brachiopods were relatively uncommon in the sections near Ziyaret, and comprised only *Aegiromena*, no doubt the " *Sowerbyella*-like brachiopods " of Kellogg's account. Very few representatives of the more abundant brachiopod faunas (including *Svobodaina*) of the Bedinan district were found, probably owing to the stratigraphically lower level of the Ziyaret strata. The highest Ordovician strata in this area could not be examined owing to the cover of Recent superficial deposits, which also obscures the junction of the Ordovician and Cretaceous rocks.

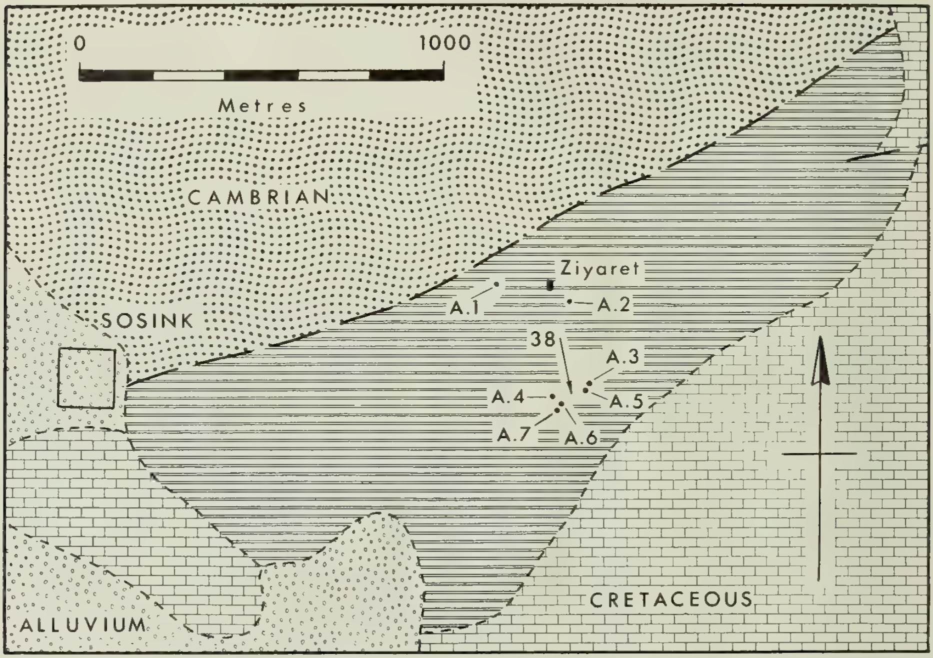


FIG. 4. Principal fossil localities in the Ordovician rocks near Sosink, 8 kilometres south-south-east of Derik. Shading as in Text-fig. 2, with addition of outcrops of Cambrian (dotted) and Cretaceous (brick pattern) rocks. Geological boundaries after Kellogg 1960.

Faunal List (for localities see Text-fig. 4)

Asaphid gen. et sp. indet. A.6.
Colpocoryphe sp. A.3.
Dalmanitina proaeva proaeva (Emmrich) A.1–6.
Dionide formosa (Barrande) *anatolica* subsp. nov. A.3, 5, 7.
Marrolithoides orthogonius sp. nov. A.3–6.
?*Neseuretus* (*Neseuretinus*) *turcicus* subgen. et sp. nov. A.3.
Selenopeltis inermis (Beyrich) *angusticeps* subsp. nov. A.2, 3.
Aegiromena sp. A.2, 3, 4, 5, 7.
Svobodaina sp. A.3.
Sinuites (s.l.) sp. A.2, 6.
Redonia sp. A.3.
Ribeiria sp. A.3.
Bivalve indet. A.3.
Miscellaneous Ostracoda A.3, 6.
Hyolithids indet. A.3.
Plumulites sp. A.3, 4, 5, 6, 7.
Climacograptus sp. A.3.
Lasiograptus sp. A.2.
Orthocone cephalopod indet. A.3.

IV. AGE AND RELATIONSHIPS OF THE BEDINAN FAUNAS

Perhaps the most obvious feature of the Beninan shelly faunas is their overall resemblance to those of the Bohemian region, even though the relevant Turkish forms are, for the most part, at least subspecifically distinct. The Bohemian trilobite species identical with, or most closely related to, those of the Bedinan Formation are as follows: *Dalmanitina proaeva proaeva* (Emmrich), *Kloucekia phillipsii* (Barrande), *Dionide formosa* (Barrande) and *Selenopeltis inermis inermis* (Beyrich) [= *S. buchi* (Barrande)]. From accounts of the Bohemian faunas published by Havlíˇeck *et al.* (1958) and Šnajdr (1956) the ranges of these species are as follows: *D. proaeva proaeva*, Černín & Chlustina Beds; *Dionide formosa*, Černín Beds. The lists of Havlíček *et al.* show that *Kloucekia phillipsii* occurs only in the Chlustina Beds, its type horizon, but Šnajdr records it from the Drabov Beds (basal Caradoc Series) to the Chlustina Beds. *Selenopeltis inermis* has an extended vertical range and is alleged to occur as low as the Dobrotiva Beds (Llandeilo Series) and as high as the Bohdalec Beds (topmost Caradoc). The species has been recorded (as *S. buchi*) by Seilacher (1963) from the Sinat Shales, of unspecified Ordovician age, in northern Iraq, not far to the east of the Bedinan district.

In the Bedinan Formation *Dalmanitina proaeva proaeva* and *Kloucekia phillipsii euroa* occur throughout most of the fossiliferous sequence, an association suggesting that a tentative correlation with the combined Černín Beds and Chlustina Beds is not unreasonable. *Dionide formosa anatolica* has been found only in the Sosink district, in the lower part of the Bedinan Formation, and this geological horizon may not be far removed from that of *D. formosa* in the Černín Beds.

The evidence of the remaining trilobites is inconclusive, though the species present may be potentially useful for correlation when other Tethyan faunas are better documented. *Marrolithoides* is a Llandeilo/Caradoc genus in north-western France and the Anglo-Welsh area, where *Cryptolithus* is found in the Llanvirn and Llandeilo Series, whilst *Colpocoryphe* is a fairly common constituent of Mediterranean faunas ranging in age from Arenig to Caradoc Series. *Brongniartella* is, above all, a genus of the Caradoc Series in the Anglo-Welsh area, most of its other occurrences in Europe and Scandinavia being as a single, widespread species, *B. platynota* (Dalman), in the Ashgill Series. Its appearance in the Turkish Caradoc is rather unexpected but suggests an easterly migration along the Tethys during Caradoc times, though its subsequent migration and development are far from clear. The new subgenus *Neseuretus* (*Neseuretinus*) is of particular interest as it may provide a link between European and Asian faunas of generally similar age. The horizon of *N.* (*Neseuretinus*) *birmanicus* (Reed) in Burma and China is obscure in terms of modern stratigraphy, but it forms part of Whittington's (1966 : 723) Caradoc *Encrinurella* fauna. As pointed out elsewhere (Dean 1967) the age of the *Encrinurella* fauna may vary within the Caradoc Series, and is apparently greatest in Australasia.

The number of graptolites found during the present field-work was disappointingly small and the specimens are poorly preserved, but Dr. Strachan has kindly examined them and supplied notes on their horizon. They include *Diplograptus* (s.s.) sp. and *Climacograptus* sp. near Sosink. Although little precise information can be given regarding their zonal position, Dr. Strachan considers all the specimens to be of Caradoc age. " They are not pre-*gracilis* [Zone], could well be *multidens-clingani* [Zone], and are unlikely to be *linearis* [Zone] or later " (personal communication). Such an assessment accords well with the evidence of the trilobites, and supports a broad correlation with the Černín and Chlustina Beds, sub-divisions which, in Bohemia, are overlain by the Bohdalec Beds, regarded as the topmost part of the Caradoc Series (Bouček 1937 : 454).

All the other animal groups represented in the Bedinan Formation are in a minority by comparison with the trilobites. Brachiopods may be locally abundant, particularly in the higher strata west of Bedinan, but are often poorly-preserved. They include, *inter al.*, the genera *Aegiromena* and *Svobodaina* (Havlíček 1950 : 38, 109), indicating once more a close relationship with the Caradoc Series of Bohemia. The remainder of the fauna consists mainly of molluscs, represented by the almost ubiquitous *Redonia* and nuculids, together with gastropods, usually smooth forms of bellerophontid type generally resembling *Sinuites*. The alleged phyllopod genus *Ribeiria* was found uncommonly near both Bedinan and Sosink. Hyolithids occur in small numbers but are usually incomplete and poorly-preserved, whilst plates of the machaeridian genera *Lepidocoleus* and *Plumulites* are not uncommon. All these groups form an assemblage broadly similar to many others in the Tethyan region, extending as far west as Portugal, Normandy, Wales and, probably, Florida. Such assemblages range in age from Arenig to Caradoc Series and many of the constituents, apart from the more obvious, diagnostic forms, exhibit relatively little morphological change, although a modern revision of the molluscs is still awaited.

V. SYSTEMATIC DESCRIPTIONS

Family **RAPHIOPHORIDAE** Angelin, 1854

Genus ***AMPYX*** Dalman, 1828

Ampyx nitidus sp. nov.

(Pl. 5, figs. 5, 8–11)

DIAGNOSIS. *Ampyx* with broad, pear-shaped glabella, its greatest breadth measured one-third of distance from base of frontal spine to occipital furrow. Only traces of glabellar lobes. Triangular fixigenae relatively short, about one and a half times as broad as long. Pair of large pits near outer ends of posterior border furrow. Pygidium short, with median length about one-third frontal breadth. Axis poorly defined with at least two small axial rings. Side lobes have one pair deep, straight, pleural furrows.

HOLOTYPE. It.1181 (Pl. 5, fig. 8).

PARATYPES. It.1180 (Pl. 5, fig. 10); It.1207 (Pl. 5, fig. 5); It.1208 (Pl. 5, fig. 9); It.1209 (Pl. 5, fig. 11).

LOCALITY AND HORIZON. The species was found at only one locality, B.2, south-west of Bedinan, in the lower part of the Bedinan Formation there. It was accompanied by *Cryptolithus*? *inferus*, *Neseuretus* (*Neseuretinus*) *turcicus* and inarticulate brachiopods (listed as *Schizocrania* sp.).

DESCRIPTION. The cranidium, excluding the frontal spine which has not been found preserved, is subtriangular in plan with median length about half of the basal breadth. The glabella is subtrapezoidal in outline, bluntly pointed frontally, with the sides diverging forwards at about 50°. The maximum breadth is slightly more than three-quarters of the median length of the glabella (excluding frontal spine and occipital ring), and is measured across the intersection of the sides and the front of the fixigenae. About one-third of the glabella lies in front of the line of maximum breadth. Although there has been some dorsal compression, there can be no doubt that the original glabellar outline expanded forwards markedly. The glabella stands a little higher than the fixigenae and is separated from them by broad, shallow, slightly curved axial furrows which become deeper frontally and curve inwards, though the region of the anterior border is not preserved. The glabella carries only poorly-defined traces of lobation. A transverse, basal segment, representing the 1p glabellar lobes, is delimited by a pair of shallow 1p glabellar furrows which run inwards and slightly forwards to join medially, where they become almost obsolete. Immediately in front of the basal glabellar segment are traces of a pair of semi-elliptical 2p glabellar lobes. The fixigenae are subtriangular and of moderate size, with about one-third of the length of the glabella projecting in front of them. The margins are straight and run backwards slightly for a short distance from the axial furrows as far as the facial sutures. Each of the latter meets the cephalic margin at an acute angle and from there pursues a gently flexuous course, at first slightly concave outwards and then slightly convex, before cutting the posterior border immediately outside a large, slot-like pit in the posterior border furrow. The occipital ring is low, moderately broad (*sag.*), continuous with, but projecting backwards beyond, the transversely straight, ridgelike posterior border. The occipital furrow is mostly shallow but deepens a little abaxially where it joins the posterior border furrow. The latter is broad (*exsag.*) and shallow with a pair of pits sited near the outer ends [see above].

A single incomplete hypostoma was found (Pl. 5, fig. 10), so small as to probably represent an immature individual. The median body is moderately and almost uniformly convex, bounded posteriorly and posterolaterally by a narrow, slightly raised border. The posterior margin is almost transversely straight, as are the posterior portions of the lateral margins which converge slightly backwards and meet the posterior margin at rounded, obtuse angles.

The thorax is not known.

One example of the pygidium was found, apparently only slightly compressed. The outline is transversely subelliptical, about three times as broad as long, its frontal margin transversely straight except medially, where a small articulating half-ring projects forwards slightly. The axis is triangular in plan, with the sides coverging backwards at about 35°. It is not strongly defined, stands only a little higher than the side-lobes, and reaches the posterior margin ; two axial rings are visible. The side-lobes carry one pair of deep, straight pleural furrows, extending almost to the margins and delimiting a pair of half-ribs which are declined anterolaterally to form a pair of small facets. The impression of a broad doublure is covered with fine terrace-lines which run subparallel to the margin.

Discussion. *Ampyx nitidus* is one of the youngest species assigned to the genus and exhibits marked differences from early forms of *Ampyx*. The type species, *A. nasutus* Dalman (see Whittington 1950 : 554) has a narrower, less divergent glabellar outline, with a smaller proportion of the glabella projecting in front of the fixigenae, which are also relatively longer. The Swedish species, which is of Upper Arenig age, possesses a pair of pits at the outer ends of the posterior border furrow, as does *A. nitidus*. This feature is not seen, or is less well developed, in species such as *Ampyx linleyensis* Whittard (1955 : 18), from the Lower Llanvirn of the Shelve Inlier, and the Shropshire form is also distinguished by its broader glabella with smaller frontal projection, as well as by the well differentiated glabellar and alar lobes. The pygidium of the Turkish species is relatively shorter than that of *Ampyx nasutus* or *A. linleyensis*, has a more rounded margin, and the axis is less well defined and segmented. The hypostoma of *A. nasutus* is not yet known but that of *A. linleyensis* has a pear-shaped outline, posterior wings and lateral notches not seen in the incomplete specimen attributed here to *A. nitidus*.

Ampyx virginiensis Cooper (1953 : 16), from the Lower Edinburg Formation (early Caradoc) of Virginia, has been redescribed in detail by Whittington (1959 : 465). Like *Ampyx nitidus* it has a relatively short, rounded pygidium but differs from the Turkish species in having a shorter frontal projection of the glabella, as well as more distinct glabellar furrows and a strong development of alar lobes. As far as can be judged the hypostoma of *A. nitidus* appears to be more like that of *A. virginiensis* than that of *A. linleyensis*. *Ampyx camurus* Raymond (Whittington 1959, pl. 30, figs. 15, 18, 19), also from the Edinburg Formation, has a cranidium generally similar to that of *A. nitidus* but the glabella is slightly narrower and the fixigenae are relatively longer, whilst the pygidium has a more triangular outline.

Ampyx nitidus bears a general resemblance to *A. abnormalis* Yi (1957 : 557, pl. 5, figs. 3*a–e*), also of Caradoc age, from the Yangtze-Gorge District of China, but the Turkish species may be distinguished by its slightly longer cephalon, with the front of the glabella extending a little farther in front of the fixigenae, and the slightly shorter, more rounded pygidium.

Family **TRINUCLEIDAE** Hawle & Corda, 1847

Subfamily **CRYPTOLITHINAE** Angelin, 1854

Marrolithoides, nowadays accorded generic rank, was erected by Williams (1948 : 78) as a subgenus to differentiate *Marrolithus*-like trilobites in which the lateral cephalic margins are approximately parallel, the arrangement of fringe-pits is relatively simple, and the cephalic fringe is uninflated anterolaterally, except in gerontic forms. Since then Whittard (1956 : 49, 63) has redefined the genus and transferred William's species *M. anomalis*, regarded by its author as atypical of *Marrolithoides*, to *Marrolithus*. According to Whittard the criteria for distinguishing *Marrolithoides* are now as follows : (a) the cephalic outline is subrectangular ; (b) the fringe is not distended anterolaterally and there is no abnormal increase in pit-diameter there ; (c) auxiliary pits are generally present in E_1 ; (d) E_1, I_1 and, sometimes, I_2 are continuous frontally ; (e) I_1–I_2 pseudogirder is almost as strongly developed as the normal E_1–I_1 girder. Specimens from the Bedinan Formation which possess these features, together with unmistakable anterolateral angulation of the cephalic outline, may therefore reasonably be assigned to *Marrolithoides*. Individuals of this type occur in the succession east of Sosink and also at locality B.3, in the lowest part of the succession exposed near Bedinan, but the numerous trinucleids collected suggest that such generic limits as those listed above may be somewhat arbitrary. The angular cephala of B.3 are associated with smaller individuals—apparently immature examples of the same species—in which the outline is rounded anterolaterally. Similarly-rounded cephala, but of relatively large size and therefore presumably adult forms, occur at locality B.1 as well as from B.5 to the top of the succession near Bedinan. Trinucleid cephala possessing such rounded outlines together with a single row of pits external to the girder would normally be termed *Cryptolithus* sensu stricto, and the name is used here, with some doubt, for most of the Turkish specimens described. The latter, in general, show a greater development of concentric rows of pits than is customary for such forms as the type species *C. tesselatus* Green, from the Caradoc of eastern North America, and it is likely that the affinities of the Turkish specimens lie, rather, with species in Bohemia as well as those described by Whittard (1958 : 72–77) from the Llanvirn and Llandeilo Series of the Shelve Inlier. The latter group of species was said by Whittard to be distinct from those in North America, but there is as yet no evidence that they merit generic separation. On the basis of the above criteria the trinucleids of the lowest Bedinan Formation are placed in *Marrolithoides*. The remainder are attributed questionably to *Cryptolithus* and there is a small stratigraphical overlap of the two genera in the lower strata exposed south-west of Bedinan. The terminology used in the following descriptions is that of Whittard (1955 : 27) and the pit counts refer to half the cephalic fringe.

Genus ***MARROLITHOIDES*** Williams, 1948

Marrolithoides orthogonius sp. nov.

(Pl. 1, figs. 1–9)

Diagnosis. *Marrolithoides* with subrectangular cephalic outline and three concentric rows of pits [E_1, I_{1-2}] developed frontally, except for small irregular group near sagittal line. E_1, I_2 pits of similar size ; I_1 pits slightly larger. I_{3-5} present, but I_6 represented by only few small pits. Average pit-count : $E_1 + e_1$ 26, $I_1 + i_1$ 21, $I_2 + i_2$ 21, $I_3 + i_3$ 18, $I_4 + i_4$ 17, $I_5 + i_5$ about 14 or 15 [for variation see description].

Holotype. It.1200 (Pl. 1, fig. 6).

Paratypes. It.747 (Pl. 1, fig. 4) ; It.749 (Pl. 1, fig. 8) ; It.760 ; It.762 (Pl. 1, fig. 7) ; It.803 (Pl. 1, fig. 2) ; It.806 (Pl. 1, fig. 5) ; It.812 (Pl. 1, fig. 1) ; It.818 (Pl. 1, fig. 9) ; It.819 (Pl. 1, fig. 3).

Localities and horizons. The holotype and most of the paratypes are from the Bedinan Formation at locality A.3 in the section near Ziyaret, some 1300 m. east of Sosink. This locality yielded the species in greatest abundance, some 60 specimens, whilst more than 20 were obtained from the same section at locality A.6, whence came two of the paratypes. Localities A.4 and A.5 produced only a few specimens of *M. orthogonius*.

Description. The cephalon is approximately subrectangular in outline, more than twice as broad as long (excluding spines), though the proportions are obviously affected by dorsal compression, so that the cephalic fringe now appears flattened, in contrast to its original, steep declination outwards. The frontal margin, gently convex forwards in plan, forms a broad curve and meets at an obtuse angle the lateral margins, which are almost straight and converge forwards gently. The degree of anterolateral angulation seems to be genuinely variable, ranging from a broad curve, particularly in smaller specimens, to a relatively sharp angle. In one case (Pl. 1, fig. 5) the angle is marked by a blunt projection developed from the margin at about R 16. The glabella is about twice as long as broad, stands high above the cheek-lobes, and narrows backwards slightly to a shallow occipital furrow which deepens laterally into a pair of apodemal pits. The best-preserved specimens show a small, median tubercle which is slightly more conspicuous on the internal than on the external mould. The glabella extends forwards a little beyond the cheek-lobes, from which it is separated by deep, straight, axial furrows, so that the cephalic fringe narrows (*sag.*) frontally. Each axial furrow contains a prominent hypostomal pit sited just behind the pitted fringe. Some specimens show faint, lateral indentations of the glabella, suggesting almost obsolete glabellar furrows, but in most the glabellar margins are entire. One of the smallest specimens (Meraspis, Degree unknown, Pl. 1, fig. 7) shows, in addition to traces of eye-ridges, a conspicuous development of alar lobes ; the latter are less obvious on both an example of Meraspis, Degree 4 (Pl. 1, fig. 9) and slightly larger cephala (Pl. 1, figs. 1, 2), and are absent from the presumed adults. A deep occipital furrow separates the glabella from the narrow (*sag.*) occipital ring, which is steeply inclined backwards, produced upwards and back to form a thorn-like occipital spine approximately half the length of the glabella. The posterior border is narrow (*exsag.*) and transversely almost straight as far as the fulcra, where it flexes backwards a little way, becoming flange-like and indented to form a pair of articulating sockets. Beyond the fulcra the posterior margins of the cephalic fringe are almost transversely straight, and the backward projections of the fringe (so-called posterior wings) which characterize certain of the Bedinan Formation trinucleids, and are sometimes very large, are here noticeably absent. The small Meraspis figured here (Pl. 1, fig. 7) shows the genal angles set well forwards, in front of the line of the posterior border furrow. This feature is shared with other cryptolithinids, and the position of the genal angles moved progressively backwards during ontogeny. Only incomplete examples have been found showing the librigenal spines ; these are directed backwards and slightly outwards from the genal angles, and apparently resemble those found in other members of the Cryptolithinae. Many specimens exhibit a conspicuous reticulation of the cephalic test, but in others it is less well developed or even, occasionally, almost absent. It is not yet clear whether such variation is original or due to vagaries of preservation. When present the reticulation is confined to the cheek-lobes and the axial portion of the glabella (see Pl. 1, fig. 1).

The cephalic fringe is narrow (*sag.*) in front of the glabella, becomes broader laterally, attaining its maximum opposite the antero-lateral portions of the cheek-lobes, and narrows a little laterally, finally broadening again near the posterior border, where it expands around the posterolateral extremities of the cheek-lobes. Three concentric rows of pits, E_1 and I_{1-2}, are almost continuous frontally, except for a small, irregular area near the sagittal line which appears to be of specific importance. At this point small cephala (see Pl. 1, fig. 4) exhibit a group of three pits arranged in a triangle with apex directed backwards. The anterior two pits form part of E_1, whilst the hindmost pit may probably be regarded as part of I_1, though sometimes it occupies a position between I_1 and I_2. In larger cephala (see Pl. 1, fig. 8) the group of three pits is replaced by one of four pits, three of them corresponding to, and arranged in-line with, E_1, and the centre pit of the three arranged radially with the fourth pit so as to form a radial row, R0, coincident with the sagittal line. Additional concentric rows of pits are developed as follows : I_3 from R3 or R4; I_4, from R6 or R7 (occasionally R5) ; I_5 from R9 (less commonly from R10 or R11) ; I_6, when present, is developed only as a few pits in the area denoted by R11 to R15, or thereabouts. The pits of E_1 and I_2 are of similar size and show almost no variation in size over the whole of their length. The pits of I_1 are slightly bigger, also uniform in size, and a low ridge is developed between E_1 and I_1, particularly anterolaterally. Although all the material is somewhat compressed there is a suggestion that the corresponding portions of I_1 may have been raised slightly above the adjacent rows, but there is no indication of distended pits such as are found in the analogous parts of *Marrolithus*. The pits internal to I_2 diminish slowly in size towards the cheek-lobes and are often set in shallow radial sulci ; the latter may be exaggerated by crushing, which may also overemphasize the radial extension of such sulci to include, apparently, pits of I_1 and I_2 ; The number of pits along the posterior border of the fringe is generally about eight, in addition to a single, larger, apodemal pit. Apart from the area of irregular pitting near the sagittal line described above, the arrangement of pits is remarkably orderly, with a strong radial arrangement persisting from R_1 to within a few pits of the genal angles. Auxiliary pits occur only uncommonly, though an occasional specimen may have an extra pit or so on one side of the cephalon and not on the other. An example is shown in Pl. 1, fig. 6, with E_1 containing two intercalated pits, between R3 and R4, and between R8 and R9 ; these occur only on the right side of the cephalon. The number of pits present in the fringe is as follows, the first number indicates the number of pits most commonly found, the second, in brackets, shows the range of variation : E_1 26 (23–28), I_1 21 (20–24, rarely 25), I_2 21 (20–22, rarely 23), I_3 18 (17–19, one specimen with 21), I_4 17 (15–18), I_5 approx. 14–15, but most material not suitably preserved ; I_6 either not developed, or present only as a few pits from a point varying from R11 to R15.

The ventral side of the cephalic fringe carries an E_1/I_1 girder which is well defined anteriorly, less so laterally, and finally becomes more pronounced again just before attaining the genal angle, where it forms a well-marked ridge which is continued along the librigenal spine. Between I_1 and I_2, and between I_2 and I_3, are pseudogirders, each successively a little less strongly developed than the last but nevertheless well defined, and traces of additional pseudogirders occur between the remaining I rows.

The thorax is known only from poorly-preserved material of characteristic cryptolithinid form, that is to say it contains six segments, the first of them macropleural. Each pleura ends in a blunt point, directed posterolaterally, and carries a broad (*exsag.*), straight, shallow, pleural furrow which runs gently backwards abaxially from the axial furrow almost to the pleural tip, near which it curves backwards slightly and dies out.

The pygidium is subtriangular in plan with the transversely straight anterior margin broken only by the articulating half-ring. The lateral margins, defined by a small, raised ridge, are straight and widely divergent over the posterior two-thirds but then curve forwards to the anterolateral angles. The axis stands slightly higher than the flattened side-lobes and is gently rounded in cross-section. The anterior two-fifths of the axis carry three well-defined axial rings, gently curved and convex forwards in plan. The rings, which are not sharply delimited laterally, are separated by ring furrows which are continuous laterally with markedly shallower furrows traversing the side-lobes and running gently backwards to reach the marginal rim. The remainder of the axis has traces of several small, poorly-defined rings, and the tip merges into the marginal rim, here less sharply defined. The side-lobes carry only traces of furrows in addition to those continuous with the first three ring furrows. The pygidium of Meraspis, Degree 4 (Pl. 1, fig. 9) is semielliptical in plan and proportionately shorter than that of the adult trilobite.

DISCUSSION. For convenience the species of *Marrolithoides* are discussed together (see p. 100).

Marrolithoides laticirrus sp. nov.

(Pl. 2, figs. 1, 3, 5, 9, 11, 13, 14)

DIAGNOSIS. *Marrolithoides* with cephalic outline broadly rounded frontally, angular anterolaterally. Large posterolateral extensions of fringe. Reticulation of glabella and cheek lobes characteristic in both small and, to lesser degree, larger individuals. Broad cephalic fringe contains four continuous concentric rows of pits (E_1, I_{1-3}) frontally; remaining rows well developed. Pit count relatively high, average as follows: E_1 36–38, I_1 27–30, I_2 26–30, I_3 29, I_4 up to 26, I_5 21, small development of I_6. Pygidium with about nine axial rings and five pairs pleural ribs.

HOLOTYPE. It.683 (Pl. 2, fig. 5).

PARATYPES. It.690 (Pl. 2, fig. 11); It.706 (Pl. 2, fig. 3); It.707 (Pl. 2, fig. 1); It.708 (Pl. 2, fig. 13); It.712 (Pl. 2, fig. 14); It.738 (Pl. 2, fig. 9).

LOCALITIES AND HORIZONS. The type material is from locality B.3, south-west of Bedinan, where it was found in moderate abundance (sample of 22 specimens) associated with *Dalmanitina*, *Kloucekia* and a single example of *Cryptolithus*? *inferus*. A few specimens from B.4, about 12 m. higher in the succession, differ from the type material in only small details and are considered to fall within the limits of variation for the species.

DESCRIPTION. The cephalon has a maximum breadth about two and a quarter times the median length. The lateral margins are straight or very slightly concave, and typically almost parallel, although some specimens exhibit a slight divergence or convergence which may have been exaggerated by crushing. The anterior margin of the cephalon is arched forwards, moderately in smaller cephala but more strongly in larger specimens. One of the latter, the holotype (Pl. 2, fig. 5), shows the lateral and anterior margins meeting at obtuse but sharply defined angles which are in line with the highest point of the glabella, about one-third of the distance from the front of the glabella. The cephalic fringe is notably broad, with a frontal breadth (*sag.*) [measured on dorsally compressed specimens] equal to two-fifths of the glabellar length. Its maximum breadth is anterolaterally, behind which it narrows a little, just in front of the line of the posterior border furrow, before expanding again towards the genal angles, which are set well back, at the end of large genal prolongations. At the genal angles the lower lamella of the fringe is produced backwards to form a pair of prismatic librigenal spines, curving gently outwards at first and then inwards, with a length at least two and a half times that of the glabella. There is a strong, concentric arrangement of fringe-pits, usually with four continuous rows (E_1, I_{1-3}) developed in front of the glabella, but occasionally only three rows (E_1, I_{1-2}). I_4 may be developed as far forwards as R3. The pits of I_1 are conspicuously the largest and maintain an almost uniform size to the genal angle. The pits of I_2 are slightly smaller whilst those of E_1 and E_3 are slightly smaller still. The pits of subsequent I rows diminish steadily in size inwards from the girder. All the specimens are moderately compressed dorsally but most show a development of a sharp concentric ridge sited anterolaterally between E_1 and I_1, and extending from about R6 to R2 or thereabouts. Some show a suggestion of a smaller I_{1-2} ridge anterolaterally. These structures suggest that the uncrushed cranidia may originally have had the anterolateral portions of I_1 raised slightly above neighbouring rows. The number of pits in each of the rows I_{1-4} is fairly uniform but the number in E_1 is conspicuously higher and many of the pits there do not fit easily into a radial pattern. The region of the fringe internal to the girder exhibits a strong radial arrangement, comprising from seventeen to nineteen radii which cover an area extending to within a few pits (generally 3 or 4) of the posterior border. A sample of 15 specimens from the type locality yielded the following counts: $E_1 + e_1$ 36–38 [in small cephala 29–34, rarely 26]; $I_1 + i_1$ 26–30 [occasionally 23–25]; $I_2 + i_2$ 26–30 [occasionally 22–25]; $I_3 + i_3$ 26–29 [occasionally 23–25]; $I_4 + i_4$ is well developed in the holotype, with 27 pits from R3, but small cephala may have as few as 18 pits; $I_5 + i_5$ 10–19 [from R8 in a large cephalon, from R12 to R14 in a small one]; I_6 only a trace, perhaps a few pits from about R14–R16. At locality B.4 a small sample of three cephala was obtained. These have a smaller pit count (33–34) for $E_1 + e_1$ than the type material but are otherwise similar and are attributed to the same species. The glabellar outline is clavate, expanded frontally where the maximum breadth is slightly less than two-thirds of the median length. Two pairs of lateral depressions represent the glabellar furrows, and the frontal glabellar lobe does not invade the cephalic fringe to any marked degree. The cheek-lobes are plump, quadrant-shaped, and their dorsal surface, like that of the axial portion of the glabella, is covered with a fine, mesh-like pattern of raised ridges. An occasional specimen shows a small, median tubercle at the apex of the glabella. The small occipital ring is produced backwards and upwards to form a small, sharp occipital spine. On the ventral surface of the fringe the girder is moderately developed, only slightly stronger than the pseudogirders I_1/I_2 and I_2/I_3.

The remainder of the exoskeleton is generally similar to that found in other members of the subfamily, with six thoracic segments of characteristic type. The subtriangular pygidium has slightly flexed, steeply declined margins surmounted by a thin, dorsal rim. There are about nine small axial rings separated by ring furrows, the anterior members of which cross the shallow axial furrows and are continuous with five or six shallow pleural furrows.

DISCUSSION. *Marrolithoides orthogonius* is the earliest-occurring trinucleid species yet known in the Bedinan Formation, and was found only in the upper part of the section east of Sosink. The not inconsiderable thickness of underlying shales there has yet to yield trinucleids, but the beds in question are inadequately exposed. *M. orthogonius* has not been found outside the Ziyaret district nor, conversely, have any of the trinucleid species from Bedinan been found elsewhere. This may be accounted for by the fact that the Ziyaret strata are probably older than the lowest seen west of Bedinan, and if any overlap of the sections occurs one would expect it to involve the strata under the alluvial cover adjacent to the Tertiary limestones cropping-out some 750 m. south-west of Bedinan.

Judging from Williams's drawings (1948, pl. 6, figs. 5, 7) the Welsh forms of *Marrolithoides* would appear to have very small fringe pits, but Whittard's (1956, pl. 9, fig. 3) photograph of the holotype of *M. simplex*, the type species, shows pitting of characteristic cryptolithinid dimensions, with the pits of I_1 slightly larger than the rest, a feature seen also in the Turkish material. The Anglo-Welsh species of *Marrolithoides* illustrated by Whittard (1956) possess cheek-lobes which are relatively much larger than those of the Turkish species ; consequently the cephalic fringes of the latter appear much broader although, in terms of concentric rows of pits, there is not much difference. *M. orthogonius* has a pit count not markedly different from that of *M. arcuatus* Whittard, of lowest Caradoc age at Shelve. However, the Turkish species tends to have more pits in E_1 and a larger development of I_5, whilst a triangular group of 3 or 4 pits (1 pit in I_1 and 2 or 3 pits in E_1) forms a conspicuous feature at the sagittal line. *Marrolithoides laticirrus* differs markedly from all other species of the genus in its large, broad fringe with four, almost five concentric rows of pits in front of the glabella in the adult trilobite. Also notable is the large number of pits, including intercalated ones, in E_1. The girder of *M. orthogonius* is more strongly developed than that of *M. laticirrus*, and in this respect the latter species has a ventral aspect more reminiscent of the species of *Cryptolithus* ? from the Bedinan Formation.

The French species *Trinucleus bureaui* Oehlert (1895 : 300) was described from an unspecified Ordovician horizon in Brittany. Whittard (1956 : 54) assigned *T. bureaui* to *Marrolithus* but claimed it as a composite species and drew attention to the close resemblance of some of Oehlert's illustrations to *Marrolithoides simplex* (Williams). The Breton species is in need of modern revision and, as described, may well include material attributable to both *Marrolithus* and *Marrolithoides*. Some of the specimens figured by Oehlert (e.g. 1895, pl. 1, figs. 1, 3) generally resemble *M. orthogonius* but the fringe is slightly broader anterolaterally, apparently the result of an extra concentric row of pits there, and lacks the characteristic median, triangular group of pits. The original of Oehlert's pl. 1, fig. 15 compares with a paratype of *M. orthogonius* (see Pl. 1, fig. 5) but has one more pit row and greater differentiation in pit size than the Turkish form.

Marrolithoides sp.

(Pl. 4, fig. 10)

In general, *Marrolithoides* occurs in the lower part of the Bedinan Formation, not only near Sosink but also south-west of Bedinan, where it overlaps stratigraphically with *Cryptolithus* ? *inferus*. The dominant trinucleid higher in the Bedinan Formation is *Cryptolithus*? *bedinanensis* but in some of the stratigraphically highest localities this is accompanied by uncommon forms which match best with *Marrolithoides*. The largest and most complete of these, It.881, is figured here from locality B.21. It has a greater number of concentric pit rows than *M. orthogonius*, and although there are four frontal rows as in *M. laticirrus* it is separated from that species by having a straighter anterior margin and fewer, slightly larger pits in E_1, whilst the pits of I_2 and I_3 are almost twinned near the sagittal line. I_1 is slightly raised, especially anterolaterally, and the pit-count is as follows : E_1 29 or 29 estd ; I_1 22 ; I_2 22 : I_3 22 ; I_4 20 (from R4) ; I_5 estd 17 or 18 from about R6 ; I_6 estd 16 from R10. It is not evident whether I_7 is represented. Fragmentary evidence of *Marrolithoides* was also obtained from locality B.18.

Genus ***CRYPTOLITHUS*** Green, 1832

Cryptolithus? inferus sp. nov.

(Pl. 2, figs. 2, 4, 6–8, 12)

DIAGNOSIS. *Cryptolithus*? with cephalon about twice as broad as long, its outline subangular anterolaterally and, occasionally, frontally. Cephalic fringe narrow (*sag.*) anteriorly with only three (E_1, I_{1-2}), rarely two, concentric rows of pits continuous in front of glabella. I_3 generally developed from about R4. Several intercalated pits in E_1, especially frontally and anterolaterally. Pit count relatively low, as follows : $E_1 + e_1$ 27–30 ; $I_1 + i_1$ 22–26 ; $I_2 + i_2$ 21–22 ; $I_3 + i_3$ 19 ; $I_4 + i_4$ 16–17 ; I_5 comprises about a dozen small pits in region of R10 to R18 ; I_6 not developed. Reticulation of test weak or absent in large cephala.

HOLOTYPE. It.734 (Pl. 2, fig. 8).

PARATYPE. It.735 (Pl. 2, fig. 6).

OTHER MATERIAL. It.689 (Pl. 2, fig. 12) ; It.697 (Pl. 2, fig. 7) ; It.703 (Pl. 2, fig. 4) ; It.704 (Pl. 2, fig. 2).

LOCALITIES AND HORIZONS. The holotype and paratype are from locality B.1, south-west of Bedinan, where a sample of thirteen specimens was obtained from the lowest fossiliferous portion of the Bedinan Formation seen there. Another sample, also comprising thirteen specimens, from B.2, a little higher in the succession shows a pit count for $E_1 + e_1$ which is consistently higher than that for the B.1 material (31–34 pits compared with 27–30) and is here termed *C.* cf. *inferus* (see below). The specimens from the two localities are otherwise indistinguishable. A single cranidium of *C.*? cf. *inferus* (Pl. 2, fig. 12) was found at B.3, associated with *Marrolithoides laticirrus.*

DESCRIPTION. The cephalon is about twice as broad as long, sometimes slightly broader, especially in smaller specimens, and its outline is generally well rounded except frontally, where it may be almost subangular. The glabella is high, narrow and relatively long, occupying up to five-sixths or more of the cephalic length (excluding occipital spine). It expands forwards only slightly to the rounded frontal glabellar lobe, which extends a little in front of the cheek-lobes, and the sides are bounded by almost straight axial furrows. The latter contain a pair of elongated alar lobes in immature specimens, but these structures diminished during ontogeny and are absent from the presumed adult stages. Small specimens also exhibit reticulation of the test of the cheek-lobes and centre of the glabella, but in the largest examples from the type locality this is weak or absent. On the other hand several specimens from B.2 show stronger reticulation, but this may be no more than an accident of preservation

The cephalic fringe is only moderately broad, especially frontally but also, to a lesser degree, anterolaterally and laterally. Frontally it is constricted slightly by the extension forwards of the glabella and contains three concentric rows of pits (E_1, I_{1-2}). E_1 extends to the genal angles and includes several intercalated pits, especially frontally but also anterolaterally and laterally. The pits of E_1 decrease slightly in diameter towards the genal angles, and frontally they are of approximately similar size to those of I_2. The pits of I_1 are larger than those of other rows and they, too, diminish a little anterolaterally. I_3 is developed from R3 or R4, I_4 from about R9, and I_5 from about R10 to R12. The following pit count is based on thirteen specimens from B.1: $E_1 + e_1$ 27–30; $I_1 + i_1$ 22–26; $I_2 + i_2$ 22; $I_3 + i_3$ 19; $I_4 + i_4$ 16. In the holotype I_5 consists of 12 small pits which extend from R10 to R17 or R18; the row then terminates until just in front of the posterior border furrow, where three further pits form an apparent continuation. The hindmost of these three is slightly the largest and probably represents the position of an apodeme, sited at the fulcrum and functional in the articulation of posterior border and first thoracic segment. The material available is insufficient to show whether this break in the line of I_5 is a reliable specific character, but a broadly similar break was found in at least two other specimens at the type locality. A sample of thirteen specimens from B.2, some 10 m. higher in the succession (see Text-fig. 3), gave the following pit count: $E_1 + e_1$ 31–34; $I_1 + i_1$ 22–23; $I_2 + i_2$ 21–22; $I_3 + i_3$ 19 (from R2); $I_4 + i_4$ 17 (from R4). Again, I_5 is discontinuous, with twelve to thirteen pits anterolaterally and a further two or three near the posterior border furrow. The slightly higher number of pits in E_1 is not considered to justify separation of these specimens, which are listed and figured as *Cryptolithus*? cf. *inferus* (Pl. 2, figs. 2, 4, 7). The marginal cephalic suture is of normal trinucleid type and at the genal angles the lower fringe lamella is produced posterolaterally to form a pair of librigenal spines which are long and slender, at least twice the median length of the cephalon, prismatic in cross-section, and have a longitudinal ridge continuous with the E_1/I_1 girder. In addition, two pseudogirders (I_1/I_2 and I_2/I_3) are fairly well developed, particularly frontally.

The thorax consists of six segments, the first of them slightly macropleural. The axis occupies about one-quarter of the total breadth, stands a little higher than the side-lobes, and is bounded by shallow, broad axial furrows. Each segment has a small, articulating half-ring separated from the axial ring by an articulating furrow which, on the internal mould, appears deep and broad (*sag.*) with a pair of apodemes sited abaxially. The pleurae are horizontal, parallel-sided, their tips obliquely truncated to form posterolateral points. Each pleura carries a broad, shallow, pleural furrow which runs almost straight from the anterior margin, at the axial furrow, and just fails to attain the pleural tip.

The pygidium is closely similar to that found in other species of the genus, that is is to say its outline is an Isosceles triangle, three and a half times as broad as long, with a transversely straight frontal margin and broadly divergent, faintly sinuous, lateral margins. The small axis occupies one-sixth of the frontal breadth, tapers back to the tip, and is separated from the flat side-lobes by gently curved, shallow axial furrows. There are about ten axial rings, those after the sixth being less well defined. The side-lobes carry four and a half pairs of more or less well-defined pleural ribs, occasionally with traces of a fifth pair.

A discussion of *Cryptolithus*? *inferus* and other species of the genus follows the description of *C.*? *bedinanensis* (see below).

Cryptolithus* ? *bedinanensis sp. nov.

(Pl. 3, figs. 1–7, 9 ; Pl. 4, figs. 2–9)

Diagnosis. *Cryptolithus* with cephalon (excluding librigenal spines) about twice as broad as long, its outline rounded frontally, but with sides almost straight and slightly convergent forwards. Cephalic fringe moderately broad, typically with 3 concentric rows of pits (E_1, I_{1-2}) in front of glabella, and traces of ridge between E_1 and I_1 anterolaterally. I_3 well developed, and proportion of specimens with 4 rows of pits in front of glabella increases higher in stratigraphical succession. I_{1-2} pits larger than those of adjacent rows. E_1 extends to genal angles and contains several intercalated pits. Pit count as follows : E_1 typically 32–36 but full range 26–38 ; I_1 21–27, mostly 23–27 ; I_2 21–26, mostly 23–25 ; I_3 20–25, mostly 22–25 ; I_4 16–23, mostly 18–21 ; I_5 10–18, mostly 14–18 ; I_6 6–13, mostly 7–10 ; I_7 rarely seen, with only very few pits. Thorax and pygidium of general cryptolithinid type ; latter has about ten axial rings and five and a half pairs of pleural ribs.

Holotype. It.1210 (Pl. 3, figs. 2, 3).

Paratypes. It.1211 (Pl. 3, fig. 6) ; It.1231 (Pl. 3, fig. 9).

Localities and horizons. The lowest stratigraphical occurrence of the *forma typica* is at B.6, south-west of Bedinan, where the largest sample (29 specimens) was obtained. This is also the type locality, and the greater part of the sample showed 3 pit rows in front of the glabella, though a few had 4 rows (see Pl. 3, fig. 1). The species was found subsequently throughout the remainder of the mudstone sequence of the Bedinan Formation and the proportion of specimens with 4 frontal rows of pits increased until the ratio of the two types at B.6 was almost reversed at B.16 (for data, see below).

Description. The entire dorsal exoskeleton of a slightly compressed individual is a little broader than long, approximately in the ratio 7 : 6. Just over half the median length is occupied by the cranidium, which is slightly more than twice as broad as long, the maximum breadth being measured across the genal angles. The outline is generally well rounded frontally and anterolaterally, but often straighter towards the genal angles. The glabella expands forwards gently in both height and breadth for about five-sixths of its length and then contracts to form a well-rounded frontal lobe. It is set higher than the convex cheek-lobes and is separated from them by broad, nearly straight, axial furrows. The latter become slightly broader posteriorly in the adult trilobite, and even more so in immature individuals so as to accomodate a pair of low, elongated alar lobes. As in other cryptolithinids the alar lobes became progressively smaller during ontogeny and eventually disappeared. The sides of the glabella carry two pairs of shallow impressions which represent glabellar furrows delimiting two small pairs of almost indiscernible glabellar lobes (Pl. 3, fig. 9). A shallow occipital furrow deepens abaxially to where, as seen on the internal mould, a pair of apodemes is sited behind the outer margins of the axial furrows. The occipital ring is short (*sag.*), slopes backwards gently, and is produced to form a slim occipital spine. The quadrant-shaped cheek-lobes extend forwards as far as the line of maximum breadth of the glabella. Both they and the axial portion of the glabella, which is surmounted by a small, median tubercle, frequently carry a fine, mesh-like ornamentation of raised ridges, though this is not always preserved and may not always have persisted in large individuals. In one or two immature examples a pair of fine nervures is visible on the cheek-lobes. The posterior border furrow is transversely straight, of only moderate depth, and becomes broader (*exsag.*) abaxially ; its posterior margin is more steeply inclined than the anterior. The posterior border is narrow (*exsag.*), ridge-like, transversely straight for less than half the distance from the axial furrows to the lateral margins ; it then meets a pair of fulcra and flexes down and slightly backwards around relatively small posterior prolongations of the cephalic fringe. In most trinucleids the cephalic fulcra are denoted by a pair of pits, often large, in the posterior border furrow. In the case of *Cryptolithus*? *bedinanensis* it is not clear whether they correspond to the hindmost pits of the innermost concentric row of the fringe.

The cephalic fringe is of moderate breadth frontally, where 3 or 4 concentric rows of pits (E_1 and, respectively, I_{1-2} or I_{1-3}) are developed in front of the glabella. The fringe becomes broader anterolaterally and laterally, where additional I rows soon appear. Many specimens show a low, thin ridge on the dorsal lamella, running between E_1 and I_1, and diminishing frontally and posterolaterally. It is not clear whether this was a primary structure, but such a ridge could well have been formed by dorsal compression of a fringe in which I_1 was originally set slightly higher than the adjacent rows, particularly anterolaterally (see Pl. 4, fig. 6). In the case of cephala with 3 concentric pit rows at the sagittal line, the pitted area is invaded to a greater degree by the front of the glabella, and it was thought at first that there were grounds for separating such forms from others possessing 4 complete frontal rows and little extension forwards of the glabella. All now appear to fall within the limits of variation for the species but the proportion of specimens with 4 rows (even in small cephala) increases as one ascends the succession, as shown below.

Locality	Sample	No. with 3 frontal rows	No. with 4 frontal rows
B.6	29	18	2 or 3
B.8	6	1	2
B.9	1	–	1
B.10	4	2	1
B.11	2	–	1
B.12	6	4	2
B.13	13	3	6
B.14	3	1	1
B.15	11	2	5
B.16	16	2	12
B.20	1	–	–
B.22	4	–	1

When three frontal rows of pits are present the succeeding row, I_3, is always well developed and may extend as far forwards as R3 or R4. Of the remaining rows, I_4 extends from R5 or R6 (occasionally R8 or R9), I_5 from R7 to R9 (less commonly R9 to R15), whilst I_6, although not always present in immature cephala, is usually found as far forwards as R12 to R15. I_7 is represented in only two specimens, from B.13 and B.16, by five small pits along the anterolateral boundary of each cheek-lobe. There is only one E row, extending to the genal angles and composed of numerous pits which greatly outnumber those of the I rows and are correspondingly more difficult to fit into a radial pattern. The I rows exhibit a strong radial arrangement which persists to within a few (generally 3 or 4) pits of the posterior border; usually there are 17 to 21 radii, though occasionally up to 23 in individuals with a particularly high overall pit-count. The pits of I_1 and I_2 are of about equal size, somewhat larger than those of E_1 and I_2 which are also about equisized; the pits of the remaining rows become smaller from I_4 to I_6. There are occasional deviations from this general rule and the pits of E_1 are sometimes slightly smaller than those of I_3. The following table shows the variation in the number of pits present in individual concentric rows on the cephalic fringe of *Cryptolithus*? *bedinanensis*. A blank indicates that the material available was insufficiently well-preserved to obtain a reliable figure. At B.6 and B.13 the wide range of variation is accounted for by small cephala with a lower pit-count.

Locality	No. in sample	$E_1 + e_1$	$I_1 + i_1$	$I_2 + i_2$	$I_3 + i_3$	$I_4 + i_4$	$I_5 + i_5$	$I_6 + i_6$	I_7
B.6	29	26–36 esp. 34–36	23–27	21–26 esp. 23–25	21–25 esp. 23–25	16–19	10–14	*c.* 6–8	—
B.8	6	27–31	21	22	22–23	18–19	—	*c.* 10	—
B.9	1	29	*c.* 22	—	—	—	—	—	—
B.10	4	28–33	22–24	21–23	22	18	17	*c.* 10	—
B.11	2	33	23	*c.* 24	*c.* 21	—	—	—	—
B.12	6	29–35	25–26	24–26	22–25	13–18	*c.* 17	*c.* 7	—
B.13	13	29–38 esp. 33–38	21–27 esp. 23–27	21–26 esp. 24–26	22–25	18–23	17–18	6–7	5 pits in one specimen
B.14	3	32–34	23–24	23–25	20	—	—	—	—
B.15	11	32–35	23–25	23–25	22–25	20–21	16–18	—	—
B.16	16	31–38	22–26	22–26	22–25	20–21	*c.* 16	5–6	5 pits in one specimen
B.20	1	—	*c.* 24	—	*c.* 20	—	—	—	—
B.22	4	31	*c.* 23	*c.* 23	23	20–21	*c.* 16	12–13	—

On the ventral lamella of the cephalic fringe each genal angle is produced posterolaterally to form a long, slim, gently-curved librigenal spine. Each spine is prismatic in cross-section with longitudinal ridges, the lower of which extends a little way into the pitted area of the fringe and then bifurcates. Of the branches so formed, one is developed as a thin, sharp ridge, the true girder, between E_1 and I_1; the other forms a slightly broader but lower ridge, the I_1/I_2 pseudogirder. A further pseudogirder is developed between I_2 and I_3 both frontally and anterolaterally, where it attains approximately the same dimensions as the I_1/I_2 pseudogirder. These structures are shown clearly in Pl. 3, fig. 7.

A few immature specimens of *Cryptolithus*? were collected from the Bedinan Formation and one of the smallest and best preserved is shown in Pl. 3, fig. 8. It exhibits the features characteristic of a trinucleid Meraspis, including genal angles set in front of the line of the posterior border furrow, and well-developed alar lobes. The fringe is narrow, consisting almost solely of two concentric pit rows, but the count of 23 pits is high.

The thorax consists of six segments, the first one macropleural, and is indistinguishable from other members of the genus. Material from the type locality shows clearly that the pleural tips are blunt, almost vertical, and form a virtual continuation of the form of the anterolateral margins of the pygidium (see Pl. 3, fig. 2).

The pygidium is also of the form characteristic for the genus, with a low, narrow, marginal rim. The margin is moderately declined over the median third but becomes vertical anterolaterally (see above). In apparently adult examples the axis has the first four rings well defined, with only traces of a further six rings. Small specimens generally have better-defined axial rings which appear confluent with the pleural ribs (for example Pl. 3, fig. 6, probably Meraspis, Degree 5). The side-lobes carry about five and a half pairs of ribs, separated by broad (*exsag.*), shallow, pleural furrows which broaden towards the margin.

A cranidium of unusual type (Pl. 2, fig. 10) was found at locality B.6 in association with *Cryptolithus*? *bedinanensis*. It differs from the latter in having a particularly short glabella and lateral margins which, judging from the incomplete material, must have been slightly divergent forwards. The specimen is apparently malformed and therefore difficult to compare with other species. The concentric arrangement of pits is relatively irregular frontally, where I_2 is of normal type, I_1 is deflected slightly inwards, and E_1 is displaced markedly inwards from the margin. Consequently several pits, estimated as 6 or 7 on the complete cephalon, are arranged in interradial positions frontally, almost as an incipient E_2. The specimen is listed merely as *Cryptolithus*? sp.

Another example of a pathological cranidium was found at B.13 and is figured as *Cryptolithus*? cf. *bedinanensis* (Pl. 4, fig. 1). The left side generally resembles that species but on the right side E_1 does not extend as far forwards as the axial furrow, whilst I_1 and I_2 become irregular and flex forwards, the former row reaching the cranidial margin in front of the right axial furrow.

DISCUSSION. All the species of *Cryptolithus* described by Whittard (1958 : 72 *et seq.*) from the Shelve Inlier were obtained from strata of the Llanvirn and Llandeilo Series and so are considerably older than the Turkish specimens. The Anglo-Welsh forms possess cheek lobes which are relatively large and extend forwards level with the front of the glabella, whereas in the Turkish material the glabella invariably extends beyond the cheek-lobes and often invades the pitted fringe area, to be accomodated by a flexing forwards of the inner concentric rows of pits. Another conspicuous point of difference is that the Anglo-Welsh specimens exhibit an unusually large range of pit size, those of the inner and posterolateral parts of the fringe being often exceedingly small ; The Turkish specimens have the pits of I_1 and I_2 of approximately similar size, whilst the pits of all the other rows, although smaller, are never minute. An exception to these generalizations is offered by the cephalon of " *Cryptolithus* sp. " figured by Whittard (1956, pl. 9, fig. 16) from the Lower Llanvirn of the Llandrindod area of Wales. In this form the pits are both fewer and of simpler disposition, features more reminiscent of the North American species of the genus, but only one example is yet known. Some of the specimens figured by Whittard have relatively large pygidia and in one individual (Whittard 1956, pl. 10, fig. 5) referred to *Cryptolithus* cf. *inopinatus* the pygidium seems atypical of that genus but strongly suggestive of *Lloydolithus*. It is, of course, possible that groups of trinucleids with rounded cephalic outline and one row of pits external to the girder arose independently from different genera, and may also have been differentiated geographically, but the evidence is not conclusive.

A feature of all the specimens of *Cryptolithus*? from the Bedinan Formation is the development of E_1 as a row of numerous small pits extending to the genal angle. This is reminiscent of the dorsal aspect of the cephalic fringe in *Onnia* Bancroft from the higher Caradoc Series of South Shropshire (for discussion see Dean 1960 : 127), but in the latter case the pits of E_1 and I_1 are larger than, and raised above, those of adjacent rows, whilst radial sulci are well developed from I_2 inwards. The ventral fringe surface of *Onnia* is particularly distinctive, having a strong girder with two concentric rows of pits (E_{1-2}) external to it. The girder itself is continuous with a ridge along the librigenal spine and there is a lesser development of pseudogirders between concentric rows internal to the girder, the I_1/I_2 pseudogirder at least arising from a subsidiary branch of the main structure of ridge and girder. A somewhat similar condition is found in the Turkish specimens but with only a single E row developed. In addition some examples have the girder more weakly developed so that it appears scarcely more prominent than the adjacent pseudogirders.

Cryptolithus? *inferus* shows only relatively small differences from the majority of the stratigraphically earlier members (including the types) of *C.*? *bedinanensis*, that is to say specimens which also have three concentric rows of pits in front of the glabella. *C.*? *inferus* typically has a much lower $E_1 + e_1$ count ; there is one fewer I row (this is particularly noticeable anterolaterally, where the fringe is narrower) ; and the anterior portion of E_1 consists of slightly larger pits with fewer intercalated pits.

One can postulate an evolutionary sequence within the members of *Cryptolithus*? in the Bedinan Formation. The earliest representatives, typical *C.*? *inferus*, soon acquire a slightly higher number of pits in E_1 (the latter specimens are denoted as *C.*? cf. *inferus*). Higher in the succession appears *C.*? *bedinanensis* which could have developed from *C.*? *inferus* by the addition of extra pits in almost all rows, and one concentric row internal to the girder. Further increase in the pits of I_3 led to the formation of four frontal rows in the majority of later members of the species, though the average count for individual rows does not apparently show any significant increase.

Judging from the marked Bohemian affinities of the remainder of the fauna, one might expect to compare the Bedinan trinucleids with those of Bohemia, but the lack of relevant literature makes this difficult. Whittington (1940) considered the Czech species *Trinucleus ornatus* Sternberg, *T. goldfussi* Barrande and *T. ultimus* Barrande to be identical, and redescribed them as *Onnia ornatus* (Sternberg). The type material of all these species comes from different stratigraphical horizons and Marek (1952 : 23) has pointed out that *Trinucleus ultimus*, at least, merits specific separation. Of the material illustrated by Whittington, his pl. 3, fig. 6 bears some resemblance to *Cryptolithus*? *bedinanensis* with three frontal pit rows (this paper, Pl. 3, fig. 3), but the pits of the outermost row seem fewer and rather more regularly arranged in the Czech specimen. The ventral fringe surface illustrated by Whittington (1940, pl. 3, fig. 5) shows a girder and pseudogirders which are perhaps more like those of the Turkish specimens than in *Onnia* (s.s.). The original of Whittington's pl. 3, fig. 6 was said to have been labelled as *Trinucleus goldfussi* by Barrande, and the preservation in a fine-grained, buff sandstone (Whittington 1940 : 243) suggests a possible origin in the Letná Beds of the Caradoc Series. The specimen, a cranidium, has four frontal, concentric rows of pits, several rows anterolaterally, and the lateral margins are slightly divergent forwards. The outline is reminiscent of some examples of *Marrolithoides laticirrus*, but the latter has a much larger number of pits in the outermost concentric row. Further discussion of these problems must await a modern revision of the Bohemian trinucleids.

Family **DIONIDIDAE** Gürich, 1907

Genus ***DIONIDE*** Barrande, 1847

Dionide formosa (Barrande) ***anatolica*** subsp. nov.

(Pl. 5, figs. 1–4, 6, 7, 12)

Diagnosis. Subspecies of *Dionide formosa* distinguished by following features : cephalic fringe longer (*sag.*) in front of glabella, with less well-developed marginal row of fringe-pits ; genal angles turned backwards less strongly ; pygidium proportionately shorter with slightly narrower axis, eleven to thirteen axial rings, and ten to twelve pairs pleural ribs.

Holotype. It.1061 (Pl. 5, figs. 1, 2).

Paratypes. It.1057 (Pl. 5, fig. 12) ; It.1062 (Pl. 5, fig. 6) ; It.1063 (Pl. 5, fig. 7) ; It.1178 (Pl. 5, fig. 4) ; It.1201 (Pl. 5, fig. 3).

Horizons and localities. All the type material is from the section near Ziyaret, east of Sosink, the holotype being collected from locality A.3 and the paratypes from A.3, A.5 and A.6. All these localities are believed to be in the lower part of the Bedinan Formation.

Description. The cephalon, excluding librigenal spines, is transversely almost semielliptical in plan ; the median length varies from just over one-third to almost a half of the maximum breadth, according to the degree of crushing of the specimens. The tumid glabella is roughly subquadrate in outline, the frontal lobe rounded, convex forwards and bounded by a narrow (*sag.*), deep preglabellar furrow. The posterolateral portions of the glabella are formed by a pair of large lobes, almost reniform in plan, which project slightly beyond the lateral margins of the glabella and are set below the level of the median body. They are defined by a pair of broad, shallow furrows which deepen posteriorly. One specimen (Pl. 5, fig. 4) shows the hindmost part of the glabella forming a depressed, neck-like structure, its anterior boundary immediately behind the posterior ends of the lateral lobes. As all the material is crushed, it is not clear whether this structure is primary. A narrow occipital furrow separates the glabella from a small, occipital ring which becomes shorter (*exsag.*) towards the axial furrows. Deep axial furrows separate the glabella from cheek-lobes which are almost quadrant-shaped, slightly broader than long. The cranidium is circumscribed by a narrow, low, marginal rim which is ridge-like frontally but becomes slightly broader and less inclined posterolaterally. Internal to the rim is a pitted fringe of the type characteristic for the genus, and this attains a breadth (*sag.*) frontally of between one-quarter and one-third of the length of the glabella ; this refers, of course, to compressed material and takes no account of any original inclination of the fringe. Laterally the line of demarcation between the fringe and cheek-lobes is difficult to distinguish, owing to crushing and the fact that both carry similar ornamentation. A comparable state of affairs was noted by Whittard (1958 : 99) when redescribing *Dionide jubata* Raymond. The cheek-lobes are separated by a broad (*exsag.*), posterior border furrow from a posterior border which is at first transversely straight and almost uniformly broad but then becomes narrower, turns back slightly, and finally coalesces with the hindmost, less inclined parts of the marginal rim described earlier. The surface of each cheek-lobe is traversed by a conspicuous, branched nervure which runs posterolaterally from the axial furrow, opposite the centre of the glabella, towards the genal angle. The nervure comprises thickened, irregular ridges whose development is somewhat variable. In two cases (Pl. 5, figs. 4, 6) each nervure includes two branches which coalesce near the genal angle and then die out quickly. In another (Pl. 5, fig. 3) only a single ridge is visible, whilst the holotype (Pl. 5, figs. 1, 2) shows a third, smaller branch in front of the main pair, the anterior of which is slightly the thicker. The glabella is surmounted by a conspicuous median spine, rounded in cross-section and directed backwards and slightly upwards. In the somewhat crushed holotype the length of the spine approximates to that of the cranidium, but it was probably even longer originally. A similar structure in *Dionide formosa* was illustrated by Hawle & Corda (1847, pl. 3, fig. 16) but is not usually preserved. More recently, however, Curtis (1961 : 14) has noted a Portuguese example with the spine at least 5 mm. long. One specimen from the Bedinan Formation shows the left librigena (Pl. 5, fig. 3) which, although damaged, is seen to end in a long, curved librigenal spine, the original length of which is estimated to have been at least twice that of the cephalon.

A complete thorax has not been found but one incomplete specimen (Pl. 5, fig. 3) shows four segments, the first of them markedly macropleural. Another (Pl. 5, fig. 7), with pygidium attached, has five equisized segments and is also incomplete as it lacks a macropleural segment. It is reasonable to assume that six segments would normally be present, the customary complement for the genus. The axis occupies just over one-fifth of the thoracic breadth, stands only a little higher than the side-lobes, and is bounded by narrow, almost straight, axial furrows which converge gently backwards. Each axial ring is almost rectangular in plan but ends anterolaterally in a well-defined pair of subtriangular axial lobes which are more conspicuous on the internal mould. The pleurae are transversely straight, parallel-sided, and terminate in blunt points directed posterolaterally. The breadth (*exsag.*) of the pleurae of the first, macropleural segment is about one-third that of the remaining segments. A pleural furrow runs from the anterior edge of each pleura immediately outside the axial furrow. At first it is deep and narrow, and runs almost to the centre of the pleura in a broad curve, concave forwards; it then becomes broader (*exsag.*) and shallower, and runs backwards very slightly, subparallel to the anterior margin, almost to the pleural tip, where it turns back more strongly and dies out. In the case of the macropleural first segment the pleural furrows are directed backwards more strongly, and the inner part of the anterior band (Pl. 5, fig. 3) is inflated, as in *Dionide formosa formosa* (see Whittington 1952, Text-fig. 1).

The best-preserved pygidium (Pl. 5, fig. 7) is slightly more than three times as broad as long, sub-semielliptical in outline with the anterior margin almost transversely straight. Another specimen (Pl. 5, fig. 12) appears to be proportionately longer but is more compressed. The axis, which occupies just over one-sixth of the frontal breadth, has the outline of an isosceles triangle, with well-defined straight sides converging backwards at about 20°. There are at least eleven axial rings on the first specimen, thirteen on the other, and the axis ends in a very small terminal piece just short of the posterior margin. The side-lobes have an almost flat surface which apparently becomes slightly declined near the pygidial margin, and they carry from ten to twelve pairs of pleural ribs in addition to the pair of anterior half-ribs. The well-defined pleural furrows become progressively more strongly directed backwards towards the rear of the pygidium. They are narrow and almost straight over most of their length (*tr.*) but within a short distance of the margin they turn backwards and die out, apparently without attaining the margin, so that a narrow, smooth border results. In a few cases the furrows appear to intersect the margin, but this may be due to crushing. Faint interpleural furrows are visible on the adaxial portions of the first five or so ribs but become obsolete on the remaining ribs.

Discussion. Many of the various species of *Dionide* have been enumerated and discussed during recent years by both Whittington (1952) and Whittard (1958). The Turkish specimens bear an overall resemblance to *Dionide formosa* (Barrande) and are probably of broadly similar age, but there are sufficient minor differences to warrant their separation as a new subspecies. First, the cranidium of *D. formosa formosa* has longer posterolateral genal prolongations, whilst the cephalic fringe contains a more conspicuous zone of marginal pits, larger and slightly more widely-spaced than those of *D. formosa anatolica*. Second, although the nervures of the two forms are of similar type those of the Turkish subspecies are apparently less strongly developed (judging from Whittington's illustrations, 1952, pl. 1, figs. 1, 2,

5) whilst one specimen shows an additional branch. Third, the pygidium of *D. formosa anatolica* is better segmented, with a greater number of both axial rings and pleural furrows. The conspicuous nervures of *D. formosa anatolica* easily distinguish the new subspecies from forms such as *D. jubata* Raymond (of Llanvirn age) and *D. euglypta* (Angelin) var. *quadrata* Whittard (of Caradoc age ; see Whittard 1958 : 99–102). *Dionide atra* Salter may also be of Caradoc age but has an unusually and distinctively large number of axial rings and pleural ribs (Whittard 1959 : 98). *Dionide turbulli* Whittington (1952 : 8), from the Llanvirn Series, differs from *D. formosa anatolica* in having a much broader cephalic fringe with radiating ridges, very long genal prolongations, and a pair of strongly-developed, single nervures. *Dionide hybrida* Reed (1915 : 26, pl. 5, fig. 7), from the Hwe Mawng Beds of Burma (exact age uncertain), has a cephalic outline similar to that of *D. formosa anatolica* but the glabella, which carries a median tubercle, is relatively larger, whilst the fringe is narrower and has coarser pitting, especially marginally where there is a conspicuous row of large pits. No nervures are visible in Reed's illustrations or noted in his description, but the species is founded on only a single, abraded specimen. *Dionide asiatica*, from the Ordovician of Eastern Yunnan, was founded by Kobayashi (1940 : 205) on the specimen figured by Mansuy (1912 : 37, pl. 6, figs. 2*a*, *b*) as *D. formosa*. Though broadly similar to *D. formosa formosa* and *D. formosa anatolica*, Mansuy's specimen may be distinguished by the following features : the nervures are less strongly developed ; the frontal part of the cephalic fringe is much narrower (*sag.*) ; there is a marginal row of conspicuously large fringe pits ; the pygidium is relatively longer and better segmented with twenty-five axial rings and about sixteen or seventeen pairs of pleural ribs in addition to the anterior pair of half-ribs.

Family **DALMANITIDAE** Vogdes, 1890

Genus ***DALMANITINA*** Reed, 1905

Dalmanitina proaeva proaeva (Emmrich)

(Pl. 6, figs. 1–9, 11–13 ; Pl. 7, figs. 4, 5)

1839 *Phacops proaevus* Emmrich : 25.

1956 *Dalmanitina proaeva proaeva* (Emmrich) Šnajdr : 513, pl. 4, figs. 10, 11 ; pl. 5, fig. 4. Includes discussion of species.

The species and subspecies of *Dalmanitina* in the Caradoc and Ashgill Series of Bohemia have been revised by Šnajdr (1956). They comprise, in ascending stratigraphical order : *D. proaeva cilinensis* Šnajdr, Drabov Beds ; *D. proaeva socialis* (Barrande), Letná Beds ; *D. proaeva proaeva* (Emmrich) [Šnajdr lists this only from the Chlustina Beds but Havlíček and others (1958) record it also from the underlying Černín Beds] ; and *D. proaeva grandis* (Barrande), Králův Dvůr Beds.

Three pygidia of *D. proaeva proaeva* from the Chlustina Beds, figured by Šnajdr, exhibit a small amount of variation. One (Šnajdr 1956, pl. 4, fig. 10) has ten axial rings and seven and a half pleural ribs ; another (pl. 4, fig. 11) shows nine axial rings and seven and a half pleural ribs ; whilst the third (pl. 5, fig. 4) has nine axial rings and eight and a half pleural ribs, as far as can be judged. There is a strong overall resemblance to the pygidium of *D. proaeva socialis* but the latter, while possessing a similar number of pleural ribs, has deep, relatively broad (*exsag.*) interpleural furrows, whereas those of *D. proaeva proaeva*, although distinct, are narrow and shallow.

Remains of *Dalmanitina* were found, in varying concentrations, throughout most of the Bedinan Formation, but although a certain amount of variation was observed it has proved insufficient to demonstrate the presence of more than one form. The hindmost axial rings and pleural ribs of some pygidia are not well defined but in general the range of variation is limited. The number of axial rings ranges from eight to ten (rarely traces of an eleventh), and of pleural ribs, from seven and a half to eight and a half (very rarely six, in imperfect material), figures which accord well with those for *D. proaeva proaeva*. The specimens all exhibit the broad pleural furrows and narrow interpleural furrows of the Czech species, and there are insufficient grounds for separating the two. Many of the Bedinan pygidia end in a terminal spine of varying length, usually short on the internal mould, owing to partial infilling of the internal cavity, but sometimes considerably longer on the external mould. Most of the best-preserved specimens have the spine about as long as the remainder of the pygidium, but one is exceptional in being almost one-and-a-half times as long (Pl. 7, fig. 5). The specimens are identical in all other respects.

The cephala of both *D. proaeva proaeva* and *D. proaeva socialis* are virtually identical, and are closely matched by the Turkish specimens. Two hypostomas were collected (see Pl. 6, figs. 7, 9) and although slightly compressed (one more so than the other) they resemble that of *D. proaeva socialis* illustrated by Barrande (1852, pl. 26, fig. 21).

LOCALITIES AND HORIZONS. *Dalmanitina proaeva proaeva* was found in moderate numbers in the lower part of the Bedinan Formation as seen to the east of Sosink. The lowest record was from locality A.1, but the species proved more abundant higher in the succession and was found at A.2–6, especially A.3. In the Bedinan district, presumably higher in the succession, *D. proaeva proaeva* was collected from many of the localities examined but occurred in greatest abundance in the upper part of the exposed section, covered by localities B.17–21.

Genus ***KLOUCEKIA*** Delo, 1935

Kloucekia phillipsii (Barrande) ***euroa*** subsp. nov.

(Pl. 6, fig. 10 ; Pl. 7, figs. 1–3, 6, 7, 9, 12)

DIAGNOSIS. Subspecies of *Kloucekia phillipsii* dintinguished principally by the pygidium, which has eight or nine axial rings and usually five or six pairs of pleural ribs, the latter separated from each other by deep pleural furrows carrying moderately-impressed interpleural furrows.

HOLOTYPE. It.1188 (Pl. 6, fig. 10 ; Pl. 7, figs. 9, 12).

PARATYPES. It.1187 (Pl. 7, figs. 6, 7) ; It.1189 (Pl. 7, fig. 3) ; It.1223 (Pl. 7, fig. 2) ; It.1225 (Pl. 7, fig. 1).

LOCALITIES AND HORIZONS. *K. phillipsii euroa* is one of the most abundant and characteristic trilobites of the Bedinan Formation in the Bedinan district, where it was collected from all but the lowest strata. It was not found in the Bedinan Formation east of Sosink, probably because the beds there are stratigraphically lower than those near Bedinan.

Description. The type species of *Kloucekia*, *Phacops phillipsii* Barrande (1846 : 27 ; 1852 : 557, pl. 22, figs. 1, 2, pl. 26, figs. 31–36), has recently been redescribed by Whittington (1962 : 7, text-fig. 2*a*-1) using specimens named originally by Barrande. Most of these came from Zahoržany, Bohemia, in strata once known as the Zahoržany Beds but which would nowadays be termed the Chlustina Beds, of fairly high Caradoc age. From a study of Whittington's illustrations it is clear that there are many points of resemblance between the Czech and Turkish specimens, and it has not proved possible to make a satisfactory differentiation on the basis of the cephalon and thorax. In certain cephala from the Bedinan district the glabellar furrows appear to run backwards from the axial furrows a little more strongly than do those of *K. phillipsii*, but this could easily be accounted for by variation in preservation. Some of the Turkish specimens (see especially Pl. 7, fig. 2) have a V-shaped group of tubercles on the median portion of the frontal glabellar lobe ; such a feature, though not uncommon in numerous phacopid and dalmanitid genera, is not always preserved. One of Whittington's photographs (1962, text-fig. 2*h*) shows that the cephalic doublure of *K. phillipsii* possesses a vincular furrow, and a similar structure is found in *K. phillipsii euroa* (see Pl. 7, fig. 7), though perhaps a little more strongly developed.

The most obvious differences between the two forms are to be found in the pygidium. That of *K. phillipsii* has three well-defined axial rings, followed by two fainter rings and a small terminal piece, whilst the side-lobes have four pairs of deep pleural furrows, the ribs so-formed carrying faint interpleural furrows. The pygidial axis of *K. phillipsii euroa* has five, occasionally six, well-defined axial rings, followed by three less well-defined rings (the last two ring furrows do not cross the sagittal line), and ends in a very small terminal piece. The side-lobes of the Turkish subspecies usually carry five pairs of deep pleural furrows, though sometimes there are six or, more rarely, seven pairs. Five well-developed pairs of interpleural furrows are present, which cross and indent the otherwise almost smooth, gently concave border, and there is usually a trace of a sixth pair. In general the pygidium appears to be proportionately broader than that of *K. phillipsii*, but it would be unwise to assume that this is the case when the material is usually somewhat compressed. According to Šnajdr (1956 : 39) the vertical range of *K. phillipsii* in Bohemia is from the Drabov Beds to the Chlustina Beds of the Caradoc Series, but the range of *K. phillipsii euroa* may be more restricted as it has not been found in the lowest part of the Bedinan Formation, nor has it yet been recorded outside Turkey.

Family **CHEIRURIDAE** Salter, 1864

Cheirurid gen. et. sp. ind.

(Pl. 10, fig. 3)

An incomplete thoracic segment, figured here as a latex cast, is the only representative of the cheirurids so far found in the Bedinan Formation. The specimen shows part of the axial ring, bearing a small axial lobe, delimited by an axial furrow which is shallow medially and deepens to both front and back. The pleura is parallel-sided for most of its length (*tr.*) and curves backwards, at first only gently and then more strongly, to end in a long, pointed tip, directed posterolaterally. The posterior margin has a small posterior flange, the outer part of which is not preserved, whilst an anterior flange of generally similar size expands conspicuously towards the fulcrum, where it ends in a projecting, articulating process. A shallow pleural furrow divides the pleura into two subequal bands, the anterior of which is slightly the narrower (*exsag.*). Along the pleural furrow is distributed a somewhat irregular row of almost equisized pits which begins just outside the axial furrow and ends without quite reaching the fulcrum. The material is insufficient for firm identification, but similar characters are to be seen in the thorax of *Placoparina*, a genus of Llanvirn–Llandeilo age (see Whittard 1958 : 112).

LOCALITY AND HORIZON. B.12, to the west of Bedinan, in the upper part of the Bedinan Formation exposed in the section there.

Family **SYNHOMALONOTIDAE** Kobayashi, 1963

Genus ***NESEURETUS*** Hicks, 1876

Subgenus ***NESEURETINUS*** nov.

TYPE SPECIES. *N.* (*Neseuretinus*) *turcicus* sp. nov.

DIAGNOSIS. Subgenus of *Neseuretus* distinguished by large, inclined, anterior border, with convex, transversely straight, preglabellar field delimited by conspicuous preglabellar and anterior border furrows.

DISTRIBUTION. South-eastern Turkey, Burma and southern China.

Neseuretus (***Neseuretinus***) ***turcicus*** sp. nov.

(?Pl. 7, figs. 8, 10, 11; Pl. 9, figs. 1–4)

DIAGNOSIS. As for subgenus.

HOLOTYPE. It.1179 (Pl. 9, figs. 1–3).

PARATYPE. It.1205 (Pl. 9, fig. 4).

LOCALITY AND HORIZON. The species is known with certainty from only locality B.2 at the section south-west of Bedinan, where it occurs in the lower part of the Bedinan Formation. A pygidium tentatively referred to the new form (see Pl. 7, figs. 8, 10, 11) was recovered from a probably similar horizon at locality A.3, east of Sosink.

DESCRIPTION. The species is represented by two incomplete cranidia preserved as internal and external moulds. The cranidium is moderately convex both longitudinally and transversely, with median length estimated as being slightly more than half the maximum breadth. The glabella is fairly convex, especially transversely, trapezoidal in outline, narrowing forwards so that the frontal breadth is a little more than half the basal breadth. There are four pairs of unequal glabellar lobes, diminishing in size from back to front of the glabella. The fourth lobes are the largest, their length about one-third that of the glabella, and subcircular in outline, becoming subangular anterolaterally. The fourth glabellar furrows are deeply incised, running straight inwards and slightly backwards from the axial furrows for more than half their length (*tr.*) but then turning more sharply backwards and terminating so as to leave a pair of " necks " connecting the basal lobes to the median body. There is no obvious bifurcation of the basal furrows but at their midpoints they become notably broader, with the adaxial margins steeply bevelled. The third glabellar lobes are transversely subrectangular in plan, their long axes strongly divergent forwards, and they are bounded by parallel, well-defined third glabellar furrows which are deepest adaxially. The second glabellar lobes are generally similar to, though smaller than, the third pair, but expand slightly at their outer ends, the second glabellar furrows becoming correspondingly less divergent forwards. The second, third and fourth pairs of furrows end adaxially in-line so as to leave a smooth median body which is almost parallel-sided and occupied just less than one-third of the basal glabellar breadth. Immediately in front of the second glabellar lobes the glabella narrows slightly, forming a small " step " in the outline. The first glabellar lobes are very small, about half the length (*exsag.*) of the first pair, and poorly defined frontally by first glabellar furrows which are little more than inconspicuous, shallow notches. The frontal glabellar lobe is very short, and the almost straight anterior margin has a shallow median indentation. The length (*exsag.*) of the frontal lobe diminishes markedly towards the posterolateral angles, which are less well defined than the remainder of the lobe and appear to extend abaxially just beyond the first glabellar lobes. The axial furrows are deep and broad, converging forwards in straight lines as far as the second glabellar furrows, beyond which they become more diffuse, meeting the well-defined preglabellar furrow and " anterior furrows " (see later) at a pair of broad depressions in which a pair of hypostomal pits is sited approximately opposite the mid-point of the frontal glabellar lobe. The distance from the front of the glabella to the anterior margin of the cranidium is estimated to be a little more than two-thirds of the glabellar length, that is to say it is unusually long for the genus, and is composed of two distinct parts, an anterior border and what appears to be a true preglabellar field. The anterior border is relatively large, longest (*sag.*) medially but shortening abaxially, strongly arched transversely, and fairly steeply inclined forwards to form a scoop-like front to the cranidium. The preglabellar field is well developed, its surface strongly convex, standing slightly higher than the front of the glabella. In plan it is transversely subrectangular, defined posteriorly by the almost straight preglabellar furrow and anteriorly by a deep, broad (*sag.*), anterior border furrow which is well-rounded in cross-section. The outer ends of the preglabellar field are truncated by broad (*tr.*), moderately-deep furrows which form forwards extensions of the axial furrows. Whittard (1960 : 143) introduced the term " anterior furrows " for apparently similar structures seen in other species of *Neseuretus*, defining what he described as the " anterior area ", believed by him to represent the combined anterior border and preglabellar field. In the new species there can be little doubt that a true preglabellar field is present, so that the furrows truncating it laterally are equivalent to the posterior portion of Whittard's anterior furrows. The palpebral lobes are sited opposite the second glabellar lobes and the third glabellar furrows. They are unfurrowed, strongly convex outwards in plan, stand a little lower than the adjacent parts of the glabella, and have their surface gently declined adaxially. The fixigenae are convex, arching downwards to both front and rear from the vicinity of the palpebral lobes. The gonatoparian facial suture is of the type characteristic for the genus. The surface of the test is incompletely known, but that of the anterior border is finely granulated, whilst the glabellar lobes, median body and preglabellar field carry coarser tubercles.

The remainder of the exoskeleton is unknown with certainty but a single, incomplete pygidium of appropriate type from near Sosink is referred questionably to the new species (Pl. 7, figs. 8, 10, 11). The specimen has undergone slight compression but is not unduly distorted. The axis extends to, or almost to, the tip of the pygidium and its frontal breadth is just over one third of the total breadth, which is measured just in front of centre. In addition to the articulating half-ring there are seven well-defined axial rings, followed by two less distinct rings (as far as can be judged) and a small terminal piece. The ring furrows all deepen abaxially and there is a break in the outline of the axis behind the fifth axial ring ; as far as this point the deep axial furrows converge backwards at about thirty degrees, but beyond it, to the blunt tip, they are subparallel. The side-lobes are arched-down moderately and each carries five deep pleural furrows and a sixth, fainter furrow. The anterior half-rib is deflected ventrally to form a facet of only moderate size. Each of the remaining ribs carries an interpleural furrow which is only faint over most of its length (*tr.*) but then forms a broad depression level with the abaxial ends of the adjacent pleural furrows and is directed obliquely backwards and outwards in relation to them. Although the specimen is incomplete there appears to be a smooth, narrow border.

Discussion. Numerous species of *Neseuretus* have been described, mostly from the Arenig and Llanvirn Series, and many of them have been discussed by Whittard (1960 : 138–151). Almost all can be separated from the new species by their possession of a so-called " anterior boss " in front of the glabella and their lack of a discrete preglabellar field, the only form possessing an apparently similar structure being *Neseuretus birmanicus* (Reed), a species now assigned to *N.* (*Neseuretinus*). This form was described from the Upper Naungkangyi Beds of Burma as *Calymene birmanica* by Reed (1906 : 71, pl. 5, fig. 27 ; 1915 : 44, pl. 8, figs. 1–5), and although there is still uncertainty regarding the precise geological age it may not be far removed from that of the new Turkish species. More recently Lu (1957 : 288, pl. 154, figs. 1, 2) has figured as *Synhomalonatus* (sic) *birmanica* a cranidium and pygidium from the " Middle Ordovician " of Yunnan. His illustrations are merely reproductions of two of Reed's figures of 1915, but the record is interesting in that it extends the known geographical range of *Neseuretinus* into China. In the present state of knowledge of the age of the Burmese faunas it is not possible to say whether *N.* (*N.*) *turcicus* is younger than *N.* (*N.*) *birmanicus*, but it may easily be distinguished from the latter species by the more pointed and considerably longer anterior border, the more convex preglabellar field, and the slightly narrower glabella. Reed's paper (1915) shows that *N.* (*N.*) *birmanicus* possesses a pair of small paraglabellar areas, which were not apparent in the illustrations to his 1906 publication ; it is not yet clear whether corresponding structures are present in *N.* (*N.*) *turcicus*, but the appropriate portion of the cranidium has not been found well preserved.

Family **EOHOMALONOTIDAE** Hupé, 1953

Genus ***BRONGNIARTELLA*** Reed, 1905

Brongniartella levis sp. nov.

(Pl. 8, figs. 2, 3, 6)

Diagnosis. Large species of *Brongniartella* with gently convex cranidium and scarcely defined glabella. Cranidium notably broad frontally with frontal margin only slightly convex forwards. Three pairs unequal glabellar lobes almost indistinguishable. Palpebral lobes opposite third glabellar furrows and some distance from glabella. Large, poorly-defined paraglabellar areas present.

Holotype. It.1219.

Locality and horizon. Locality B.18 in the section west of Bedinan. The horizon is in the highest part of the mudstone/shale succession of the Bedinan Formation.

Description. The new species is represented with certainty by only a single incomplete, large cranidium of markedly depressed form. The median length is 51 mm., whilst the basal breadth must have been of the order of 80 mm., although the outer parts are incomplete. The glabella is subtrapezoidal in outline with a length of 35 mm., narrowing forwards from a basal breadth of about 36 mm. (estimated). The anterior and lateral margins are only poorly defined by furrows which are little more than broad, shallow indentations of the test. Glabellar lobation is almost indiscernible, in addition to being obscured by slight crushing of the test, but there are suggestions of three pairs of glabellar lobes of markedly unequal size, the basal pair being much the largest, occupying almost half the glabellar length. The second glabellar lobes are rather less than half the length of the basal pair, whilst the first pair are notably small, probably less than half the size of the second pair. There is a gentle, outwards curvature of the axial furrows opposite the second glabellar lobes, which project a little beyond the other pairs of lobes. The anterolateral angles of the glabella are slightly swollen dorsally to form a pair of low, lobe-like structures, between which the otherwise almost straight anterior margin of the glabella is slightly indented. Similar structures have been observed elsewhere in *Brongniartella*, *Neseuretus*, and other trilobites of the Calymenacea. A slight, longitudinal, median ridging of the centre of the glabella, though probably exaggerated by crushing, is undoubtedly original in part, and represents a feature known from other species of *Brongniartella*. The preglabellar field and anterior border cannot be differentiated but are combined to form a broad (*sag.*), scoop-like structure which is moderately arched transversely, gently inclined forwards, and has its dorsal surface slightly concave. The border is separated by only a pair of shallow depressions from the anterior parts of the fixigenae, which are broad and gently declined abaxially. The anterior margin of the cranidium is broadly rounded in outline. The occipital ring is subrectangular in plan, its dorsal surface almost flat, whilst the occipital furrow is broad (*sag.*) and only lightly impressed, especially medially and abaxially where it is almost obsolete. It curves forwards slightly at its outer ends where the occipital ring passes almost imperceptibly into what remains of the posterior border. The palpebral lobes are set fairly well back, behind centre of the glabella and opposite the third glabellar furrows, and stand only slightly lower than the highest part of the cranidium. In plan they are moderately convex outwards, particularly well defined at their posterior ends, and carry no trace of palpebral furrows. The portions of the fixigenae behind the eyes are more steeply declined abaxially than are the anterior parts. They contain a pair of roughly quadrant-shaped paraglabellar areas which are large, extending forwards as far as the third glabellar furrows, but poorly defined by traces of shallow furrows. The facial suture is known from only the left anterior branch. This is sigmoidal in plan, at first curving forwards and slightly inwards from the eye, but then turning gently outwards until it reaches the cephalic border longitudinally almost in-line with the eye ; finally it sweeps inwards in a broad curve to meet the cephalic margin approximately level with the posterolateral corner of the glabella. The surface of the test is smooth except for the extreme edge of the anterior border, which is finely granulated. In addition there are widely-spaced, conspicuous pits on the fixigenae anterior to the eye, whilst similar punctae are grouped more closely on the anterior half of the frontal cephalic border, forming a zone parallel to the anterior margin.

In addition to the holotype of *Brongniartella levis*, trilobite fragments assignable to the genus were found, though at other levels and localities, in the Bedinan Formation south-west of Bedinan (see Pl. 8, figs. 1, 5). All represent smaller individuals than the holotype and none is sufficiently well preserved for certain identification. An incomplete cranidium (Pl. 8, fig. 1) may represent an immature individual of *Brongniartella levis*. A fragmentary thorax and pygidium (Pl. 8, fig. 5) appear typical for the genus but are insufficient for detailed comparison.

DISCUSSION. *Brongniartella levis* is one of a group of broadly comparable species of the genus occurring over a wide area in rocks belonging to the lower or middle parts of the Caradoc Series. In the Anglo-Welsh area *Brongniartella caradociana* Dean (1961 : 349), from the Costonian Stage [*Nemagraptus gracilis* Zone], is a slightly smaller species distinguished by having a more convex glabella, the anterior half of which becomes markedly narrower, and eyes set farther forwards than in the Turkish form. The well-known *Brongniartella bisulcata* M'Coy sp. (see Dean 1961 : 346), from a Caradoc horizon roughly contemporaneous with that of *B. levis*, has the eyes a little farther forwards than the latter species, the sides of the glabella are less convergent forwards, and the cranidium is proportionately narrower frontally. *Brongniartella platynota* (Dalman) [= *B. inexpectata* Barrande sp., see Kielan 1960 : 116] is a later form, apparently the last-known *Brongniartella*, widely distributed in the Ashgill Series of Central Europe and Scandinavia. It is easily distinguished from *B. levis* and other species of the genus by having the eyes set well forwards, whilst the glabellar outline narrows markedly and the front of the cranidium is narrower and more convex in plan.

Genus ***PLATYCORYPHE*** Foerste, 1919

Platycoryphe? sp.

(Pl. 8, fig. 4)

A single, small cranidium is tentatively assigned to *Platycoryphe*. The glabella has a basal breadth about one and a half times the median length (estd), there are three unequal pairs of glabellar lobes, and the outline narrows markedly in front of the second glabellar furrows. There is a suggestion of a right paraglabellar area but the eyes and the front of the cranidium are not preserved.

The problems of separating *Brongniartella* and *Platycoryphe* have been discussed elsewhere (Dean 1961 ; Whittington 1965). In general, the glabella of *Platycoryphe* is the more strongly segmented, a feature found in the present specimen. The specimen is, however, preserved as an internal mould, in which all cephalic furrows tend to appear deeper, and from the position of the glabellar furrows one cannot exclude the possibility of its being an immature example of *Brongniartella levis*. In the absence of the anterior border it seems better to refer the specimen, with some doubt, to *Platycoryphe*.

LOCALITY AND HORIZON. Locality B.20, in the Bedinan Formation west of Bedinan. The horizon is very close to others containing *Brongniartella* and the only other place where the two genera occur together is in South Shropshire, in the lowest subdivision of the Caradoc Series (Dean 1961).

Family **COLPOCORYPHIDAE** Hupé, 1953

Genus ***COLPOCORYPHE*** Novák *in* Perner, 1918

Colpocoryphe sp.

(Pl. 9, figs. 5, 6–10)

This characteristically Mediterranean genus is represented in the Bedinan faunas by only three specimens, one reasonably complete and two fragmentary cranidia. The glabella seems relatively narrow for the genus, with a long, transversely rectangular, frontal glabellar lobe, and the axial furrows converge forwards only gently. The Turkish species, which may be new, is probably the youngest member of the genus yet recorded. *Colpocoryphe grandis* Šnajdr sp. (1956 : 501, pl. 3, figs. 1–9), from the Drabov and Letná Beds (low Caradoc Series) of Bohemia, is broadly similar and has the eyes in a corresponding position, but differs in having more convergent axial furrows and a smaller, shorter frontal glabellar lobe.

FIGURED SPECIMENS. It.1183 (Pl. 9, fig. 5); It.1197 (Pl. 9, figs. 6–8, 10); It.1204 (Pl. 9, fig. 9).

LOCALITIES AND HORIZONS. One specimen is from locality A.3, east of Sosink, whilst the others are from B.1 and B.2, south-west of Bedinan. All these localities are believed to be in the lower part of the Bedinan Formation, and *Colpocoryphe* is one of the trilobites common to both sections.

Family **ODONTOPLEURIDAE** Burmeister, 1843

Subfamily **SELENOPELTINAE** Whittington, 1956

Genus ***SELENOPELTIS*** Hawle & Corda, 1847

Selenopeltis inermis (Beyrich) ***angusticeps*** subsp. nov.

(Pl. 10, figs. 1?, 4, 6?, 7, 8)

Diagnosis. Subspecies of *S. inermis* characterized by having narrower glabella, with sides only slightly convex in plan. Eyes set less far apart than in *S. inermis*, and palpebral lobes less convex abaxially in plan. Frontal glabellar lobe has forked appearance owing to median depression extending backwards as far as second glabellar furrows.

Holotype. It.1195 (Pl. 10, figs. 4, 7, 8).

Localities and horizons. The holotype is from locality A.2 in the section east of Sosink, whilst a small pygidium probably attributable to the same subspecies (see Pl. 10, fig. 6) was found nearby, at locality A.3. The only other specimen belonging, probably, to *S. inermis angusticeps*, is a fragmentary thorax (Pl. 10, fig. 1) from locality B.1, south-west of Bedinan. All these localities are believed to occur within the lower part of the Bedinan Formation.

Description. *Selenopeltis inermis* is a well-known species, widely distributed in Europe and the Mediterranean (Tethyan) Province, and its various subspecies extend with only relatively small modifications from the Arenig to Ashgill Series. Beyrich (1846 : 20, pl. 3, figs. *2a–c*) first described *S. inermis* from " Wessela ", Bohemia, whilst the lectotype of *Selenopeltis buchi* (Barrande 1846 : 28), a species considered by Whittard (1961 : 197) to be a subjective synonym of *S. inermis*, came from the Chlustina Beds (Caradoc Series) of Zahořany, Bohemia (see Šnajdr 1956 : 501). The holotype cranidium of *S. inermis angusticeps* is broadly comparable with published illustrations of the Bohemian species but may be distinguished by the features listed in the diagnosis. In particular the glabellar sides of the Turkish form appear almost straight by comparison, whilst the distance from the palpebral lobe to the axial line is conspicuously less than in the Czech specimens. The fragment of thorax from east of Sosink shows no diagnostic features but the small pygidium from near Bedinan, although close to that of *S. inermis inermis*, appears to be slightly longer and has a median indentation of the margin. However, this specimen is too poorly preserved for detailed comparison and neither it nor the thoracic fragment is included as type material. *S. inermis angusticeps* is not yet known from anywhere but the Sosink–Bedinan region but it is interesting to note that Seilacher (1963 : 530, fig. 2) has recorded *Selenopeltis buchi* from the Sinat Shales in northernmost Iraq, not far to the east of the Turkish outcrops.

Family **ASAPHIDAE** Burmeister, 1843

Asaphid gen. et sp. indet.

(Pl. 10, figs. 2, 5)

A single hypostoma, figured here as an internal mould and a latex cast of the corresponding external mould, is the only evidence of asaphid trilobites yet known from the Bedinan Formation. The maximum breadth, measured almost across the centre, is estimated as about three-quarters of the maximum length. The overall outline is suboval but the posterior margin is bifid, with a large, parabolic, median indentation extending for about one quarter of the length of the entire hypostoma. There is a large, subcircular, median lobe of low convexity, circumscribed by a furrow which is deepest posterolaterally. The median lobe is separated from the apex of the median indentation by a narrow (*sag.*), flat strip equal to about one tenth of the total length of the hypostoma, and ending laterally in a pair of poorly-defined maculae. Although the front of the hypostoma is incomplete, and there is no trace of anterior wings, there is a flattened lateral border, bearing terrace-lines on its dorsal surface, which is continuous with the bifurcated posterior border.

FIGURED SPECIMEN. It.1203.

LOCALITY AND HORIZON. Locality A.6, east of Sosink, the highest fossiliferous horizon in this particular section.

VI. REFERENCES

BARRANDE, J. 1846. *Notice préliminaire sur le Système Silurien et les trilobites de Bohême.* vi + 91 pp. Leipzig.

—— 1852. *Système silurien du centre de la Bohême. Ière partie. Recherches paléontologiques.* xxx + 935 pp., 51 pls. Prague & Paris.

BEYRICH, E. 1846. *Untersuchungen über Trilobiten.* 37 pp., 4 pls. Berlin.

BOUČEK, B. 1937. Stratigraphie et parallelisme de l'Ordovicien supérieur de la Bohême. *Bull. Soc. géol. Fr.*, Paris (5) **7** : 439–458, pls. A–C.

COOPER, B. N. 1953. Trilobites from the Lower Champlainian formations of the Appalachian Valley. *Mem. geol. Soc. Am.*, Washington, **55** : 1–69, pls. 1–19.

DEAN, W. T. 1961. The Ordovician trilobite faunas of South Shropshire, II. *Bull. Br. Mus. nat. Hist.* (Geol.), London, **5** : 311–358, pls. 49–55.

—— 1967. The distribution of Ordovician shelly faunas in the Tethyan region. *Systematics Assoc.*, London [in press].

EMMRICH, H. F. 1839. *De Trilobitis.* 56 pp., 1 pl. Berlin.

HAVLÍČEK, V. 1950. The Ordovician Brachiopoda from Bohemia. *Rozpr. Ústřed. Úst. geol.*, Prague, **13** : 1–133, pls. 1–13. [In Czech, with English and Russian summaries]

HAVLÍČEK, V., HORNÝ, R., CHLUPAČ, I. & ŠNAJDR, M. 1958. Fuhrer zu den Geologischen Exkursionen in das Barrandium. *Sbír. geol. Prův.*, Prague, **1** : 1–171, pls. 1–16.

KELLOGG, H. E. 1960. The geology of the Derik–Mardin area, south-eastern Turkey. *Rept Explor. Divn Amer. Overseas Petr. Ltd*, Ankara [unpublished].

KIELAN, Z. 1960. Upper Ordovician trilobites from Poland and some related forms from Bohemia and Scandinavia. *Palaeont. pol.*, Warsaw, **11** : 1–198, pls. 1–36.

KOBAYASHI, T. 1940. Notes on the Dionideidae. *Jap. J. Geol. Geogr.*, Tokyo, **17** : 203–208.

LU, Y. H. 1957. *Index fossils of China. Invertebrate, Pt.* 3, *Trilobita. Acad. sinica*, Peking : 249–294, pls. 137–155.

MANSUY, H. 1912. Étude géologique du Yun-nan Oriental. IIe partie, Paléontologie. *Mém. Serv. géol. Indoch.*, Hanoi, **1**, 2 : 1–146, pls. 1–25.

MAREK, L. 1952. Contribution to the stratigraphy and fauna of the uppermost part of the Králův Dvůr Shales (Ashgillian). *Sborník Ústřed. Úst. geol.*, Prague, **19** : 429–455, 2 pls. [In Czech, with Russian and English summaries.]

OEHLERT, D.-P. 1895. Sur les *Trinucleus* de l'Ouest de la France. *Bull. Soc. géol. Fr.*, Paris, **23** : 299–336, pls. 1, 2.

REED, F. R. C. 1906. The Lower Palaeozoic fossils of the Northern Shan States, Burma. *Palaeont. indica*, Calcutta (N.S.), **2**, 3 : 1–154, pls. 1–8.

—— 1915. Supplementary Memoir on new Ordovician and Silurian fossils from the Northern Shan States. *Palaeont. indica*, Calcutta (N.S.), **6**, 1 : 1–98, pls. 1–12.

SCHMIDT, G. C. 1965. Chart 1. Proposed Rock Unit Nomenclature, Petroleum District V, S.E. Turkey. Revised Edn. *Stratigraphic Committee, Turkish Assoc. Petroleum Geologists*, Ankara. [unpublished].

SEILACHER, A. 1963. Kaledonischer Unterbau der Irakiden. *Neues Jb. Miner. Geol. Paläont. Mh.*, Stuttgart, **10** : 527–542, figs. 1–3.

ŠNAJDR, M. 1956. The trilobites from the Drabov and Letná Beds of the Ordovician of Bohemia. *Sb. ustřed. Úst. geol.*, Prague, **22** : 477–533, pls. 32–37. [In Czech, with English and Russian summaries.]

TOLUN, N. 1960. Stratigraphy and Tectonics of southeastern Anatolia. *Rev. Fac. Sci. Univ. Istanbul*, B **25** : 201–264, 2 pls.

TOLUN, N. & TERNEK, Z. 1952. Notes géologiques sur la région de Mardin. *Türk. Jeol. Kür. Bült.* Ankara, **3** : 1–19, 5 pls.

WHITTARD, W. F. 1955. The Ordovician trilobites of the Shelve Inlier, West Shropshire, I. *Palaeontogr. Soc.* [*Monogr.*], London : 1–40, pls. 1–4.

—— 1956. The Ordovician trilobites of the Shelve Inlier, West Shropshire, II. *Palaeontogr. Soc.* [*Monogr.*], London : 41–70, pls. 5–9.

—— 1958. The Ordovician trilobites of the Shelve Inlier, West Shropshire, III. *Palaeontogr. Soc.* [*Monogr.*], London : 71–116, pls. 10–15.

—— 1959. The Ordovician trilobites of the Shelve Inlier, West Shropshire, IV. *Palaeontogr. Soc.* [*Monogr.*], London : 117–162, pls. 16–21.

—— 1961. The Ordovician trilobites of the Shelve Inlier, West Shropshire, V. *Palaeontogr. Soc.* [*Monogr.*], London : 163–196, pls. 22–25.

—— 1961. The Ordovician trilobites of the Shelve Inlier, West Shropshire, VI. *Palaeontogr. Soc.* [*Monogr.*], London : 197–228, pls. 26–33.

WHITTINGTON, H. B. 1940. On some Trinucleidae described by Joachim Barrande. *Amer. J. Sci.*, Washington, **238** : 241–259, pls. 1–4.

—— 1950. Sixteen Ordovician genotype trilobites. *J. Paleont.*, Menasha, **24** : 531–565, pls. 68–75.

—— 1952. The trilobite family Dionididae. *J. Paleont.*, Menasha, **26** : 1–11, pls. 1, 2.

—— 1959. Silicified Middle Ordovician trilobites : Remopleurididae, Trinucleidae, Raphiophoridae, Endymioniidae. *Bull. Mus. comp. Zool. Harv.*, **121** : 369–496, pls. 1–36.

—— 1962. A Monograph of the Ordovician trilobites of the Bala area, Merioneth, I. *Palaeontgr. Soc.* [*Monogr.*], London : 1–32, pls. 1–8.

—— 1965. *Platycoryphe*, an Ordovician homalonotid trilobite. *J. Paleont.*, Menasha, **39** : 487–491, pl. 64.

—— 1966. Phylogeny and distribution of Ordovician trilobites. *J. Paleont.*, Menasha, **40** : 696–737, 16 figs.

WILLIAMS, A. 1948. The Lower Ordovician Cryptolithids of the Llandeilo District. *Geol. Mag. Lond.*, **85** : 65–88, pl. 6.

YI, Y. E. 1957. The Caradocian trilobite fauna from the Yangtze-Gorges. *Acta palaeont. sinica*, Peking, **5** : 545–559, pls. 1–5.

EXPLANATION OF PLATES

All the specimens are from the Bedinan Formation and are housed in the British Museum (Natural History), the registration numbers bearing the prefix It. They are preserved as internal or external moulds, the latter usually being figured in the form of latex casts. A light coating of ammonium chloride was applied before photographing. Plates 1 to 4 by the writer; Plates 5 to 10 by Mr. P. J. Green.

PLATE 1

Marrolithoides orthogonius sp. nov. p. 96

Bedinan Formation, locality A.3, east of Sosink.

FIG. 1. Latex cast of cranidium. Paratype, It.812, ×5.

FIG. 2. Left half of internal mould of small cranidium. Paratype, It.803, ×9.

FIG. 3. Ventral side of internal mould of cephalon showing girder. Paratype, It.819, ×4.

FIG. 5. Right side of cranidium showing anterolateral angulation of outline, with small, marginal projection at about R16. It.806, ×8.

FIG. 6. Internal mould of cranidium. Holotype, It.1200, ×3.

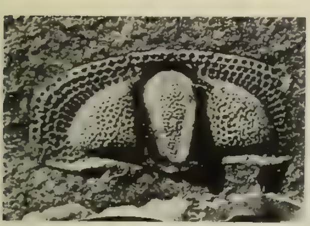
FIG. 7. Cranidium (Meraspis, Degree unknown) showing only two frontal rows of pits, increasing to three at R2 and four at about R9. Note the alar lobes and eye-ridges. Paratype, It.762, ×15.

FIG. 9. Internal mould of dorsal exoskeleton, Meraspis Degree 4. Paratype, It.818, ×8.

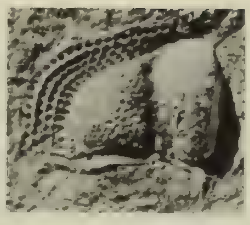
Bedinan Formation, locality A.6, east of Sosink.

FIG. 4. Group of three individuals, one enrolled, preserved as internal moulds. Paratype, It.747, ×4.

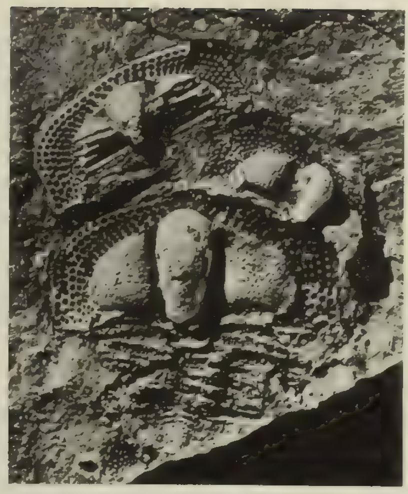
FIG. 8. Internal mould of cranidium. Note also cranidium of small Meraspis to right, and pedicle valve of a brachiopod, *Aegiromena*, in top left corner. Paratype, It.749, ×6.



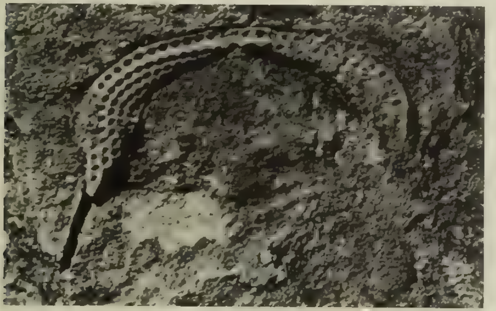
1



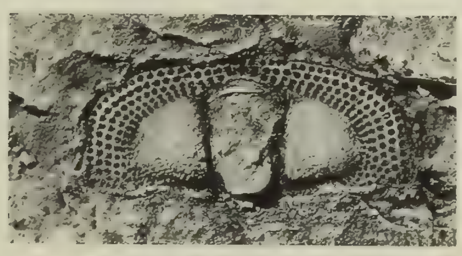
2



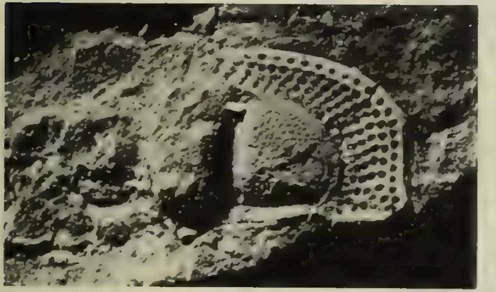
4



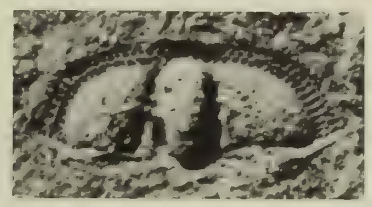
3



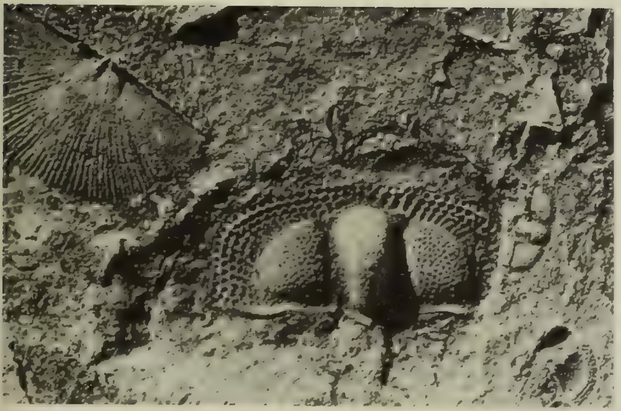
6



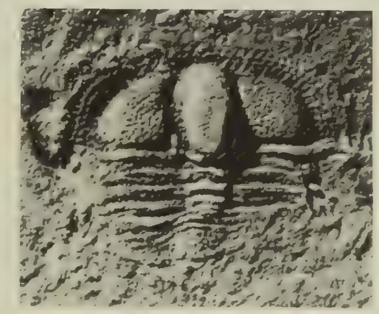
5



7



8



9

PLATE 2

Marrolithoides laticirrus sp. nov. p. 99.

Bedinan Formation, locality B.3, south-west of Bedinan.

FIG. 1. Internal mould of thorax and pygidium, with external mould of left half of cephalic fringe. Paratype, It.707, ×3.

FIG. 3. Internal mould of small cranidium. Paratype, It.706, ×8.

FIG. 5. Latex cast of cephalon with left librigenal spine. Holotype, It.683, ×3.

FIG. 11. Internal mould of incomplete cranidium. Paratype, It.690, ×5.

FIG. 13. Latex cast of cranidium. Paratype, It.708, ×4.

FIG. 14. Latex cast of small cranidium. Paratype, It.712b., ×6.

Bedinan Formation, locality B.4, south-west of Bedinan.

FIG. 9. Latex cast of small cranidium showing frontal arrangement of fringe pits. It.738b., ×6.

Cryptolithus? cf. ***inferus*** sp. nov. p. 102.

Bedinan Formation, locality B.2, south-west of Bedinan.

FIG. 2. Internal mould of thorax and pygidium. It.704, ×3.

FIG. 4. Part of cephalic fringe, showing girder. It.703, ×4.

FIG. 7. Latex cast of small cranidium. It.697, ×4.

Bedinan Formation, locality B.3, south-west of Bedinan.

FIG. 12. Internal mould of cranidium. It.689, ×4.

Cryptolithus? inferus sp. nov. p. 102.

Bedinan Formation, locality B.1, south-west of Bedinan.

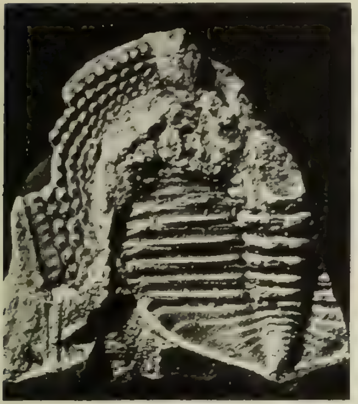
FIG. 6. External mould of ventral side of fringe. Paratype, It.735, ×2.

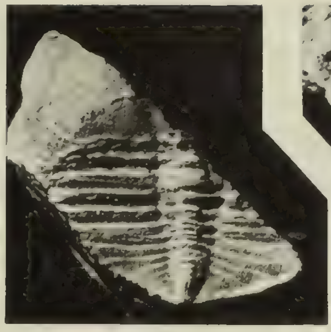
FIG. 8. Latex cast of cranidium. Holotype, It.734, ×3.

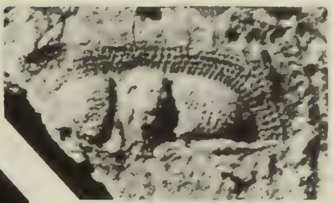
Cryptolithus? sp. p. 107.

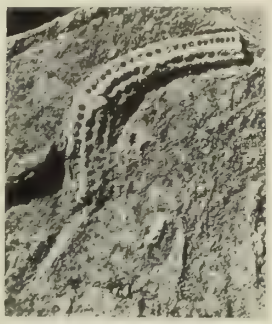
Bedinan Formation, locality B.6, south-west of Bedinan.

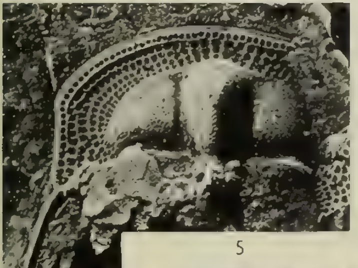
FIG. 10. Internal mould of pathological cranidium with abnormally irregular arrangement of pits frontally. It.1232, ×3.

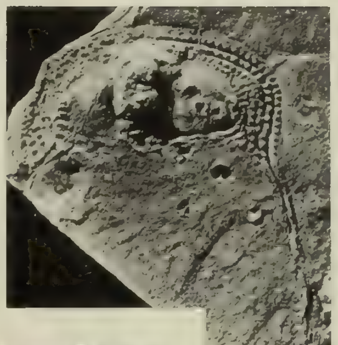

1

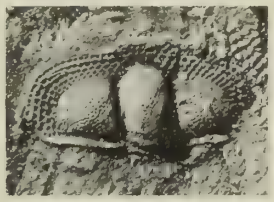

2

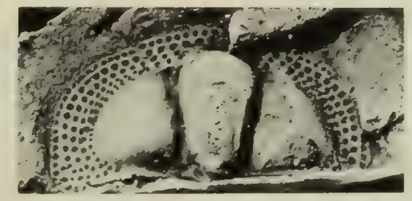

3

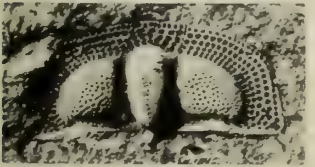

4

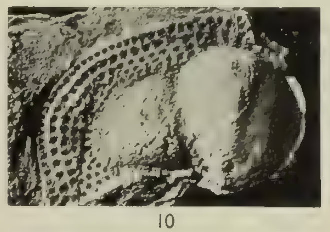

5

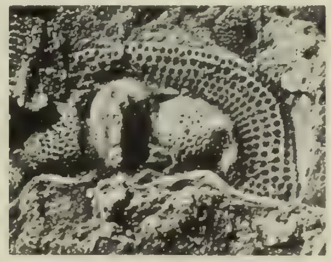

6

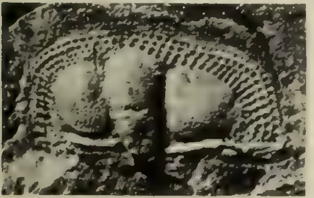

7

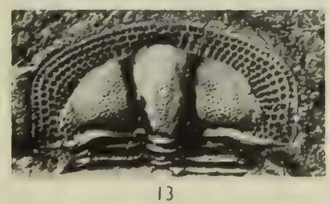

8


9


10


11


12


13

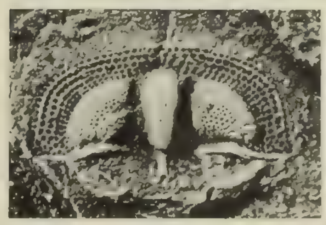

14

PLATE 3

Cryptolithus? bedinanensis sp. nov. p. 104

Bedinan Formation, locality B.6, south-west of Bedinan.

FIG. 1. Internal mould of cranidium, It.663, ×4. This is one of the earliest, rare members of the species to have 4 frontal rows of pits.

FIGS. 2, 3. Oblique posterolateral and plan views of internal mould of dorsal exoskeleton. Holotype, It.1210, ×6, shows blunt pleural tips. Fig. 3, ×4.

FIG. 6. Latex cast of two small individuals, probably Meraspis, Degree 5. Paratype, It.1211, ×5.

FIG. 9. Internal mould of incomplete cranidium. Paratype, It.1231, ×5.

Bedinan Formation, locality B.10, west of Bedinan.

FIG. 4. Internal mould of cranidium. It.713, ×3.

FIG. 7. Internal mould of ventral side of fringe, showing almost equal development of girder and two pseudogirders. It.715, ×3.

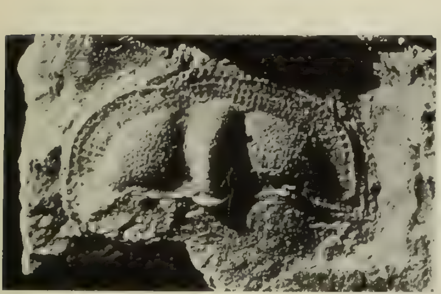
Bedinan Formation, locality B.15, west of Bedinan.

FIG. 5. Latex cast of cranidium. It.856, ×3.

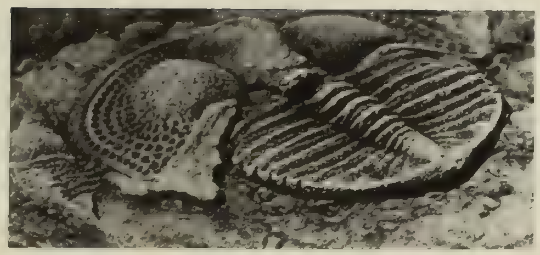
Cryptolithus? sp. juv. p. 107

Bedinan Formation, locality B.8, south-west of Bedinan.

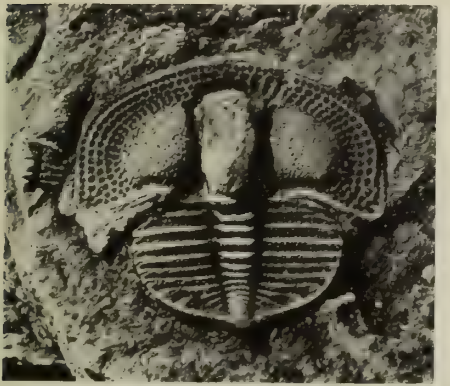
FIG. 8. Latex cast of cranidium of small Meraspis [Degree unknown], showing only two concentric rows of pits both frontally and laterally. It.718, ×15.



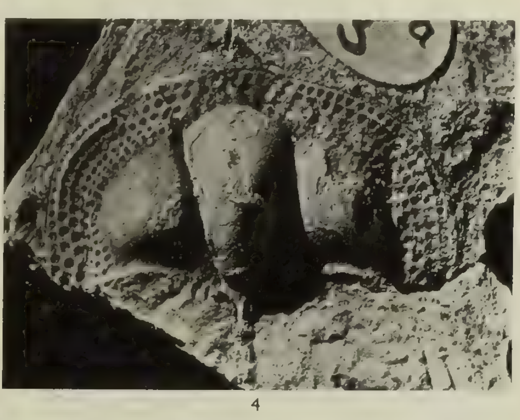
1



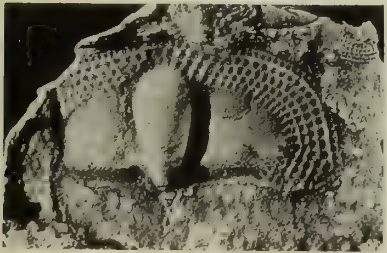
2



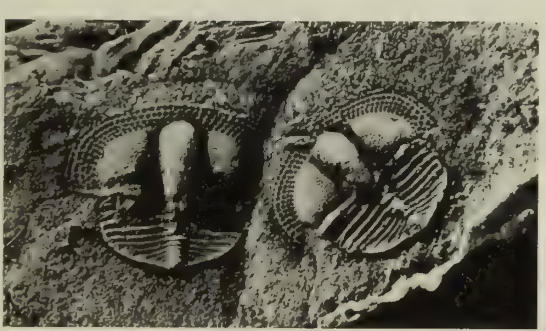
3



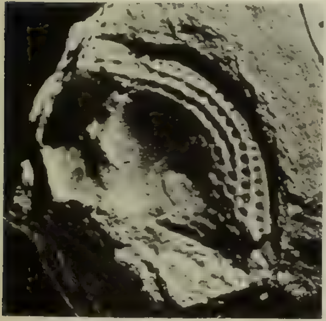
4



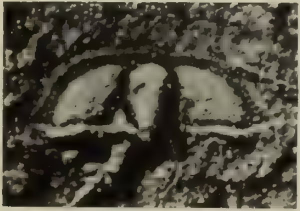
5



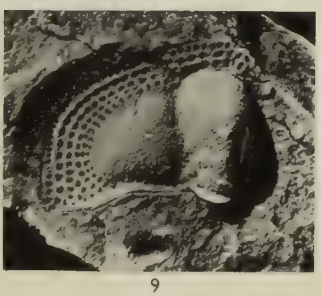
6



7



8



9

PLATE 4

Cryptolithus? cf. ***bedinanensis*** sp. nov. p. 107

Bedinan Formation, locality B.13, north-west of Bedinan.

FIG. 1. Pathological cranidium in which the regular pit arrangement is disturbed in front of the right axial furrow. It.837, ×3.

Cryptolithus? bedinanensis sp. nov. p. 104

Bedinan Formation, locality B.12, north-west of Bedinan.

FIG. 2. Latex cast of underside of fringe, showing principal girder and two weaker pseudo-girders. It.836, ×3.

FIG. 3. Internal mould of cranidium. It.834, ×4.

Bedinan Formation, locality B.16, north-west of Bedinan.

FIG. 4. Internal mould of cranidium with four rows of pits developed frontally. It.867, ×3.

Bedinan Formation, locality B.22, south-east of Bedinan.

FIG. 5. Latex cast of small cranidium. It.890, ×6.

Bedinan Formation, locality B.13, north-west of Bedinan.

FIG. 6. Internal mould of incomplete cranidium. It.1212, ×3.

FIG. 7. Internal mould of cranidium. It.1216, ×3.

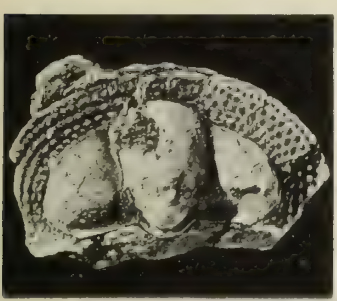
FIG. 8. Internal mould of cranidium with two attached thoracic segments. It.1215, ×3.

FIG. 9. Internal mould of small cranidium showing reticulation of the cheek-lobes. It.1214, ×5.

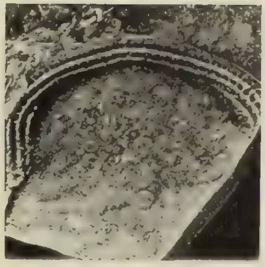
Marrolithoides sp. p. 101

Bedinan Formation, locality B.21, north-west of Bedinan.

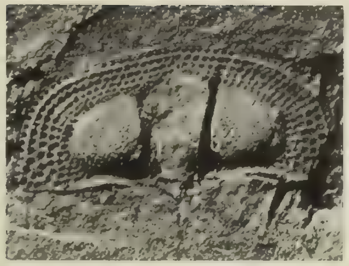
FIG. 10. Internal mould of cranidium. Note long occipital spine and anterolateral angulation of cephalic outline. It.881, ×3.



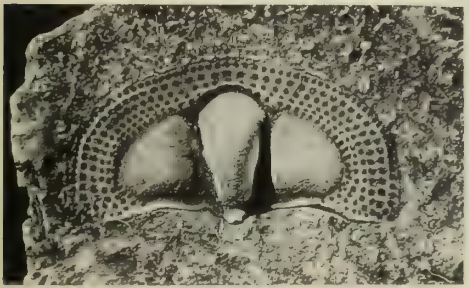
1



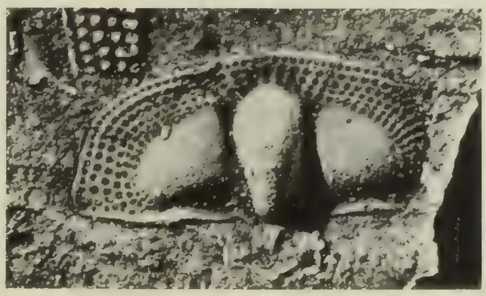
2



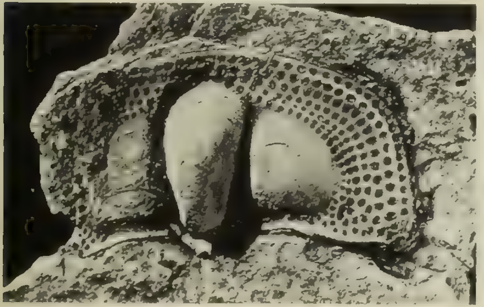
3



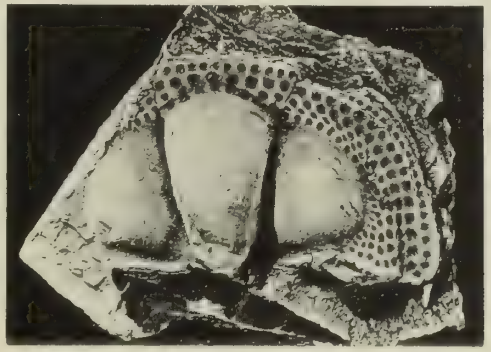
4



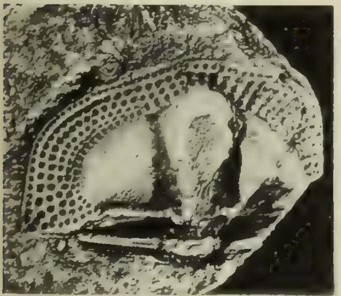
5



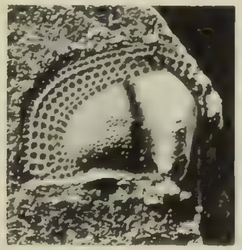
6



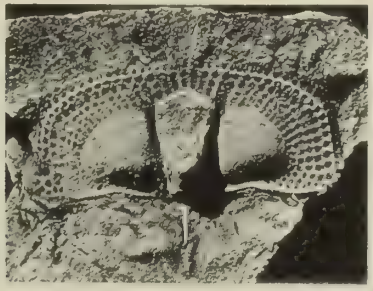
7



8



9



10

PLATE 5

Dionide formosa (Barrande) ***anatolica*** subsp. nov. p.109

Bedinan Formation, locality A.3, east of Sosink.

FIGS. 1, 2. Plan and left oblique views of cranidium showing long glabellar spine. Holotype, It.1061, ×4.

FIG. 3. Plan view of specimen showing left librigenal spine and part of thorax. Note macropleural first segment. Paratype, It.1201, ×5.

FIG. 12. Internal mould of pygidium illustrating hindmost pleural ribs. Paratype, It.1057, ×4.

Bedinan Formation, locality A.6, east of Sosink.

FIG. 4. Latex cast of cranidium. Paratype, It.1178, ×7.

Bedinan Formation, locality A.5, east of Sosink.

FIG. 6. Internal mould of cranidium. Paratype, It.1062, ×6.

FIG. 7. Internal mould of pygidium with thorax lacking first segment. Paratype, It.1063, ×6.

Ampyx nitidus sp. nov. p. 93

Bedinan Formation, locality B.2, south-west of Bedinan.

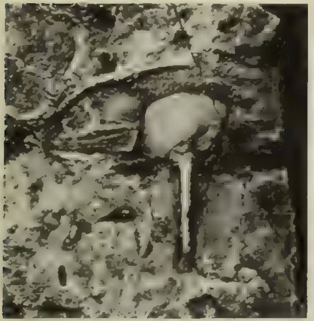
FIG. 5. Internal mould of pygidium. Paratype, It.1207, ×4.

FIG. 8. Internal mould of cranidium. Holotype, It.1181, ×3.

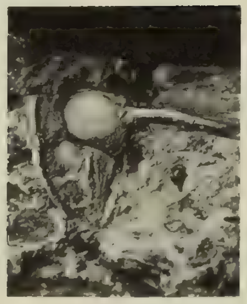
FIG. 9. Fragment of right cheek showing position of eye. Paratype, It.1208, ×4.

FIG. 10. Internal mould of small hypostoma. Paratype, It.1180, ×12.

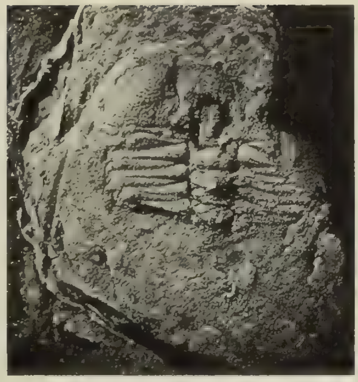
FIG. 11. Incomplete cranidium showing faint glabellar lobes. Paratype, It.1209, ×3.



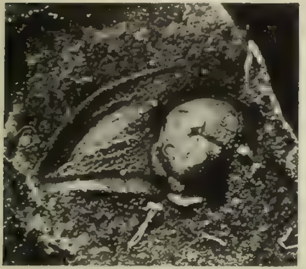
1



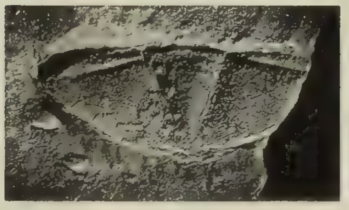
2



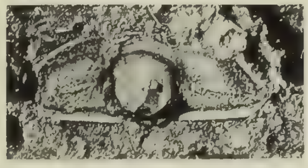
3



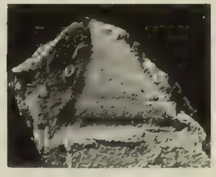
4



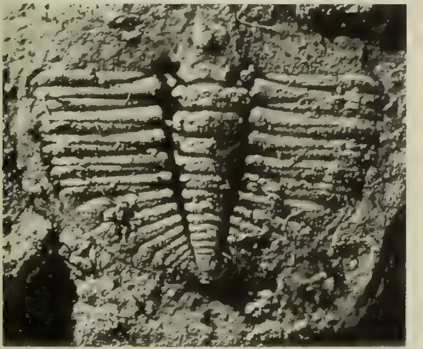
5



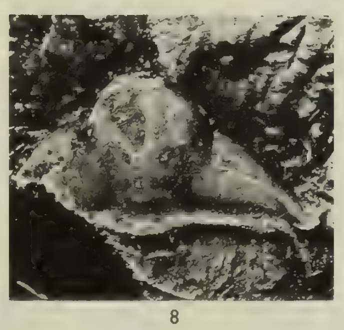
6



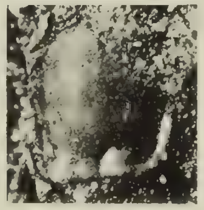
9



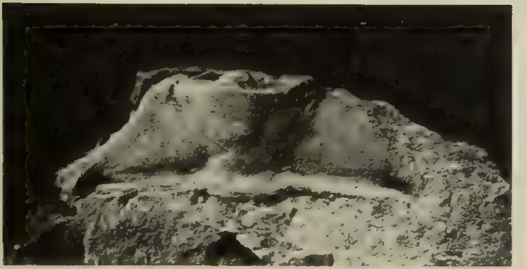
7



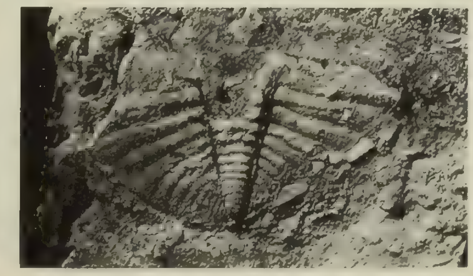
8



10



11



12

PLATE 6

Dalmanitina proaeva proaeva (Emmrich) p. 112

Bedinan Formation, locality B.21, west of Bedinan.

FIG. 1. Internal mould of cephalon. It.1224, ×1·5.
FIGS. 4, 11. Latex cast and internal mould of pygidium. It.1226, ×2.

Bedinan Formation, locality B.13, west of Bedinan.

FIG. 2. Plan view of pygidium. It.1190, ×3.

Bedinan Formation, locality B.20, west of Bedinan.

FIGS. 3, 5. Internal mould of pygidium. It.1222, ×2.

Bedinan Formation, locality B.3, west of Bedinan.

FIG. 6. Internal mould of slightly disarticulated specimen. It.1186, ×2·5.
FIG. 7. Internal mould of small hypostoma. It.1185, ×3.

Bedinan Formation, locality B.19, west of Bedinan.

FIGS. 8 12. Plan and posterior views of internal mould of pygidium. It.1193, ×1. (See also Pl. 7, fig. 5.)

Bedinan Formation, locality B.2, west of Bedinan.

FIG. 9. Internal mould of slightly compressed hypostoma. It.1182, ×2.

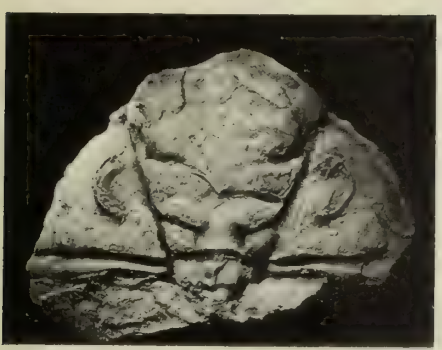
Bedinan Formation, locality B.22, west of Bedinan.

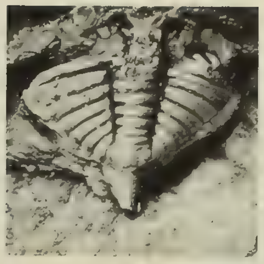
FIG. 13. Internal mould of cephalon and pygidium with long terminal spine. It.1233, ×1·5.

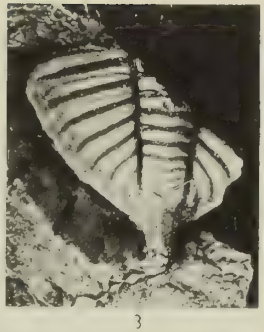
Kloucekia phillipsii (Barrande) ***euroa*** subsp. nov. p. 113

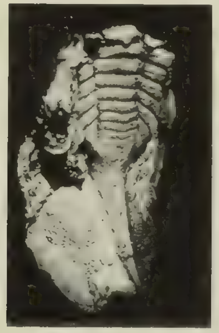
Bedinan Formation, locality B.13, south-west of Bedinan.

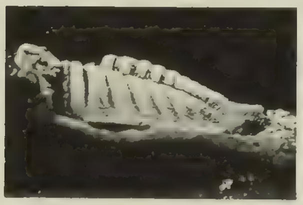
FIG. 10. Plan view of internal mould of pygidium with thorax attached. Holotype, It.1188, ×3. (See also Pl. 7, figs. 9, 12.)

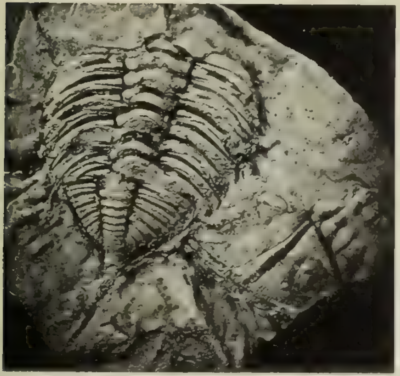

1

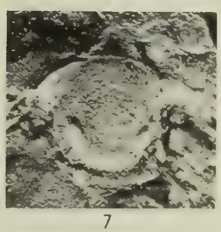

2

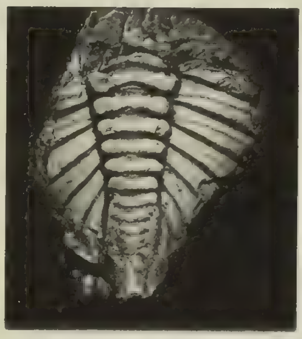

3

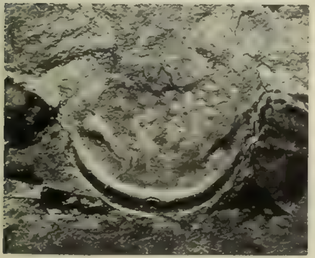

4

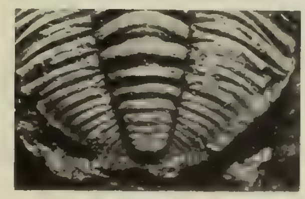

5

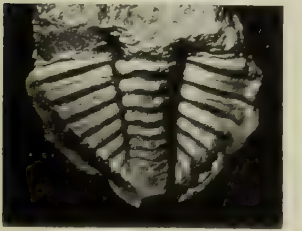

6

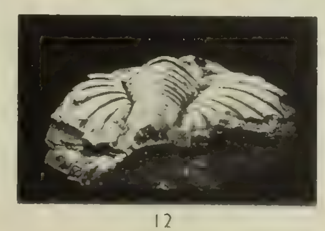

7


8


9


10


11


12

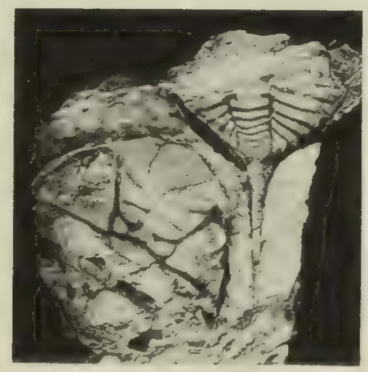

13

PLATE 7

Kloucekia phillipsii (Barrande) **euroa** subsp. nov. p. 113

Bedinan Formation, locality B.21, west of Bedinan.

FIG. 1. Internal mould of incomplete cephalon. Paratype, It.1225, ×2.

FIG. 2. Plan view of internal mould of cephalon. Paratype, It.1223, ×4.

Bedinan Formation, locality B.13, south-west of Bedinan.

FIG. 3. Internal mould of almost complete dorsal exoskeleton. Paratype, It.1189, ×1·5.

FIGS. 6, 7. Plan and oblique ventral views of cephalon. Fig. 7 shows doublure and vincular furrow. Paratype, It.1187, ×3.

FIGS. 9, 12. Thorax with attached pygidium (see also Pl. 6, fig. 10). Holotype, It.1188, ×2.

Dalmanitina proaeva proaeva (Emmrich) p. 112

Bedinan Formation, locality B.3, south-west of Bedinan.

FIG. 4. Latex cast of cranidium of Meraspis (Degree unknown). It.1018, ×12.

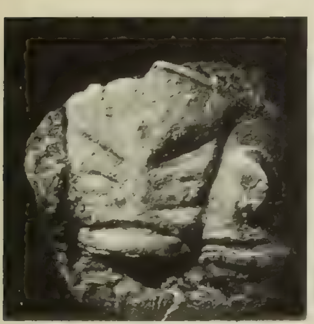
Bedinan Formation, locality B.19, west of Bedinan.

FIG. 5. Latex cast of pygidium with exceptionally long terminal spine. It.1193, ×1. (See also Pl. 6, figs. 8, 12.)

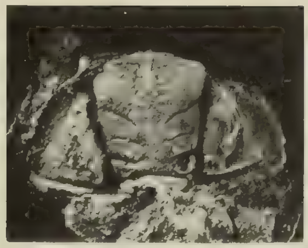
? **Neseuretus** (**Neseuretinus**) **turcicus** subgen. et sp. nov. p. 117

Bedinan Formation, locality A.3, east of Sosink.

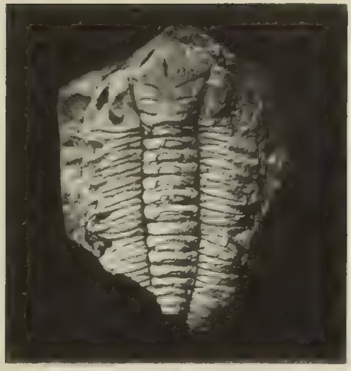
FIGS. 8, 10, 11. Posterior, plan and right lateral views of internal mould of pygidium. It.1196. ×2.



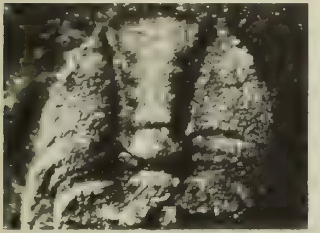
1



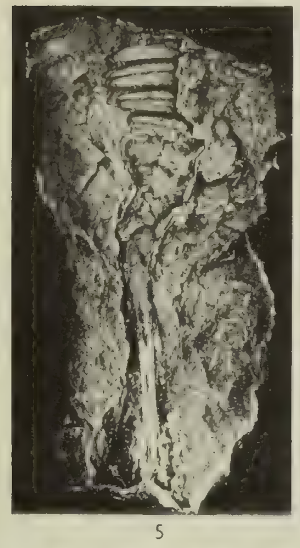
2



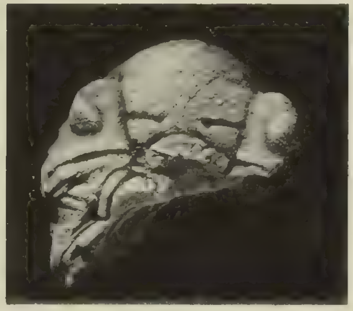
3



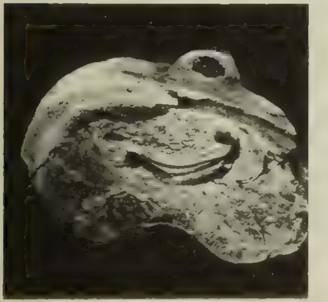
4



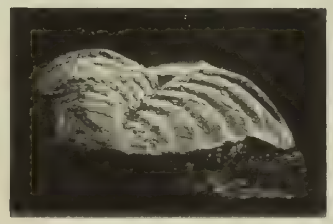
5



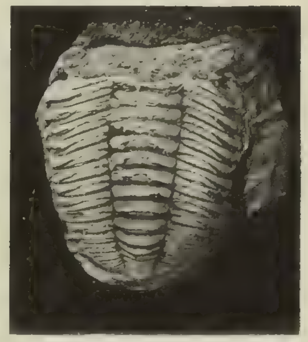
6



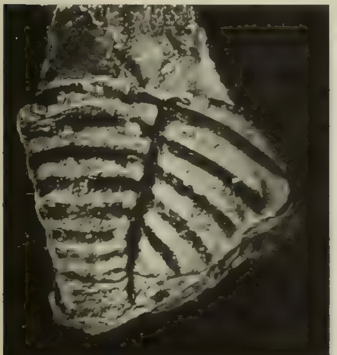
7



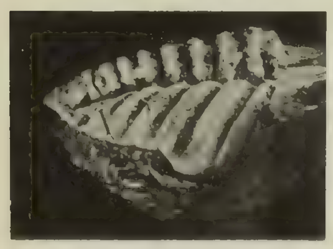
8



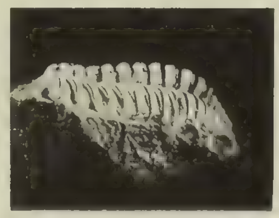
9



10



11



12

PLATE 8

Brongniartella sp. p. 119

Bedinan Formation, locality B.13, south-west of Bedinan.

FIG. 1. Internal mould of damaged cranidium. It.1217, ×1·5.

Bedinan Formation, locality B.19, south-west of Bedinan.

FIG. 5. Internal mould of thorax and pygidium. It.1220, ×2·5.

Brongniartella levis sp. nov. p. 118

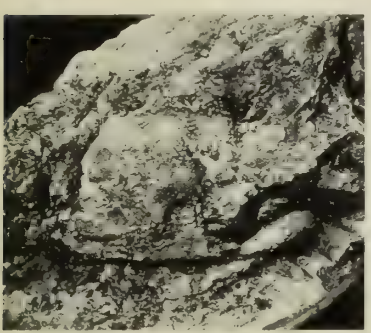
Bedinan Formation, locality B.18, south-west of Bedinan.

FIGS. 2, 3, 6. Anterior, left lateral and plan views of incomplete, large cranidium. Holotype. It.1219, ×1·25.

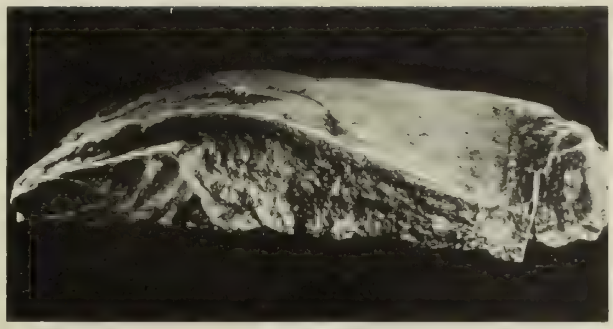
Platycoryphe ? sp. p. 120

Bedinan Formation, locality B.20, south-west of Bedinan.

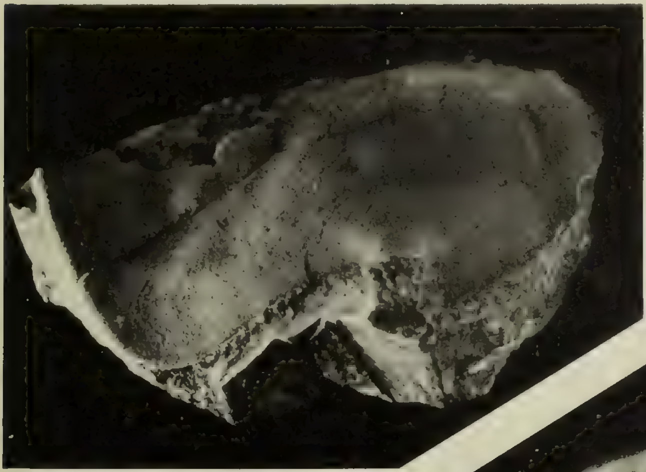
FIG. 4. Internal mould of incomplete cranidium. It.1221, ×3.



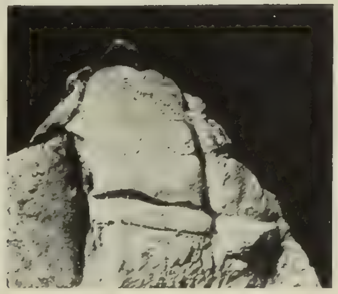
1



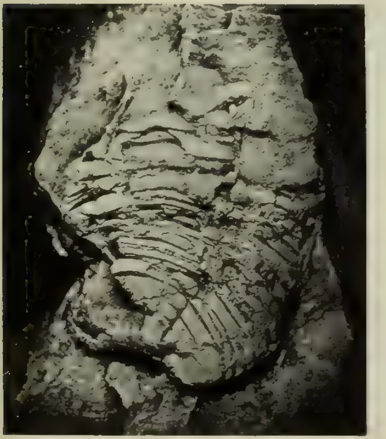
2



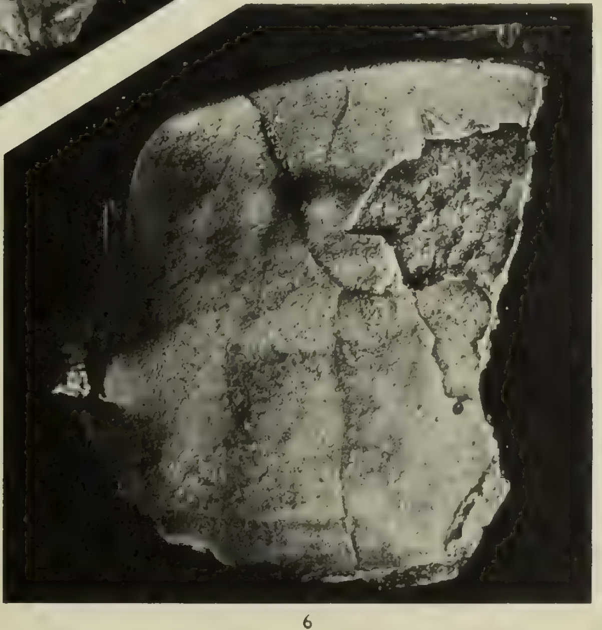
3



4



5



6

PLATE 9

Neseuretus* (*Neseuretinus*) *turcicus subgen. et sp. nov. p. 115

Bedinan Formation, locality B.2, south-west of Bedinan.

FIGS. 1–3. Plan, left lateral and oblique anterolateral views of latex cast of incomplete cranidium, showing convex preglabellar field and large, inclined, anterior border. Holotype, It.1179, ×3.

FIG. 4. Plan view of internal mould of incomplete cranidium lacking marginal portion of anterior border. Paratype, It.1205, ×2.

Colpocoryphe sp. p. 120

Bedinan Formation, locality B.2, south-west of Bedinan.

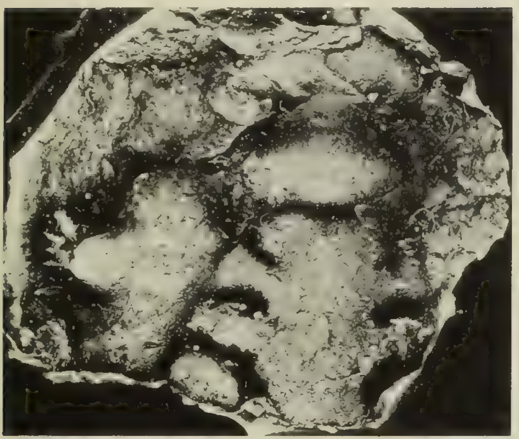
FIG. 5. Latex cast of frontal portion of fragmentary cranidium. It.1183, ×2.

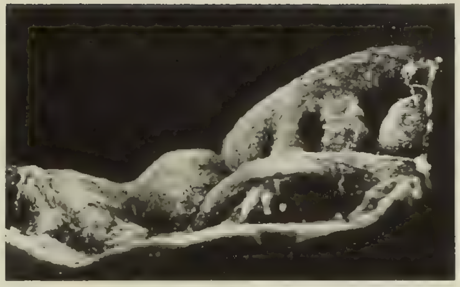
Bedinan Formation, locality A.3, east of Sosink.

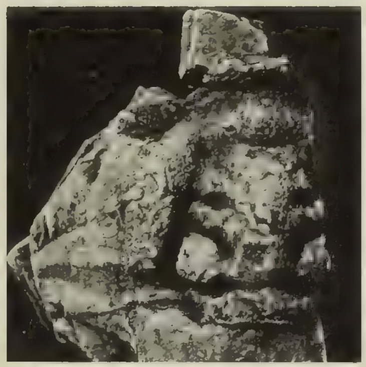
FIGS. 6, 10, latex cast and figs. 7, 8, corresponding internal mould, of small cranidium. It.1197, ×6.

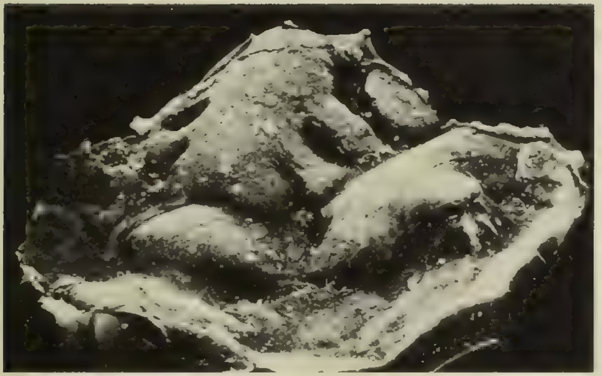
Bedinan Formation, locality B.1, south-west of Bedinan.

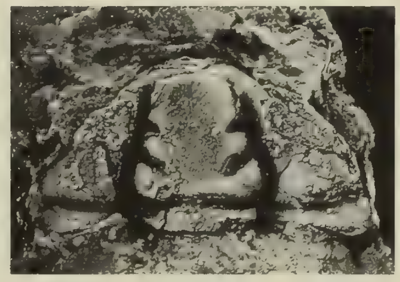
FIG. 9. Posterior half of glabella, an internal mould. It.1204, ×2·5.

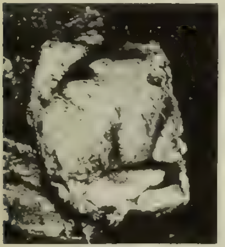

1

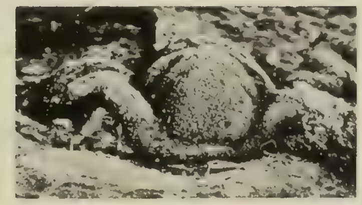

2

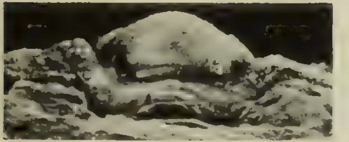

4

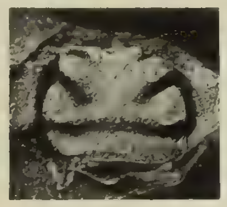

3


7


5


6


8


9

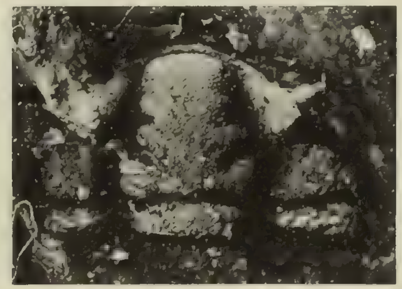

10

PLATE 10

Selenopeltis inermis (Beyrich) ***angusticeps*** subsp. nov. p. 121

Bedinan Formation, locality B.1, south-west of Bedinan.

? FIG. 1. Internal mould of fragment of thorax. It.1206, ×2·5.

Bedinan Formation, locality A.2, east of Sosink.

FIGS. 4, 7, 8. Left lateral, anterior and plan views of internal mould of cranidium. Holotype, It.1195, ×3.

Bedinan Formation, locality A.3, east of Sosink.

? FIG. 6. Internal mould of small pygidium. It.1198, ×5.

Asaphid gen. et sp. ind. p. 121

Bedinan Formation, locality A.6, east of Sosink.

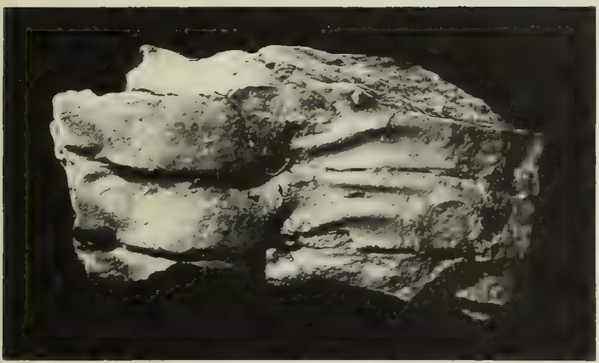
FIGS. 2, 5. Latex cast and internal mould of hypostoma, showing indented posterior margin. It.1203, ×2·5.

Cheirurid gen. et sp. ind. p. 114

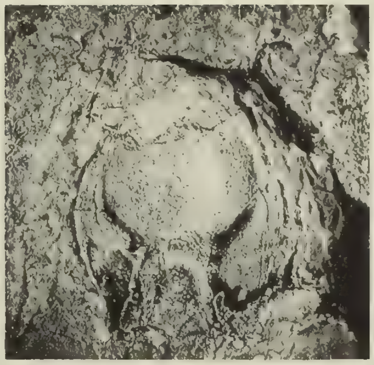
Bedinan Formation, locality B.12, south-west of Bedinan.

FIG. 3. Latex cast of left half of thoracic segment, showing furrow with pits, and anterior flange terminating in articulating process. It.1213, ×2·5.

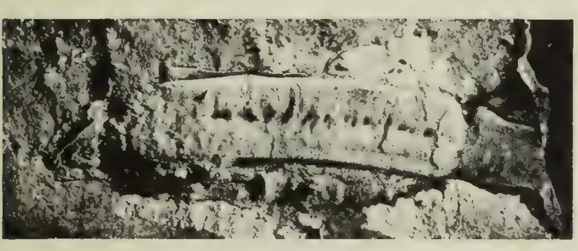
PLATE 10



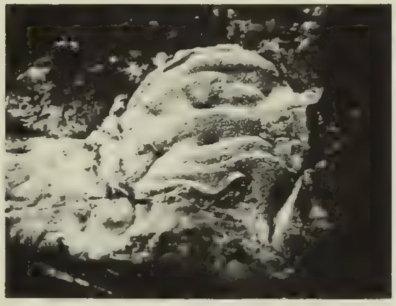
1



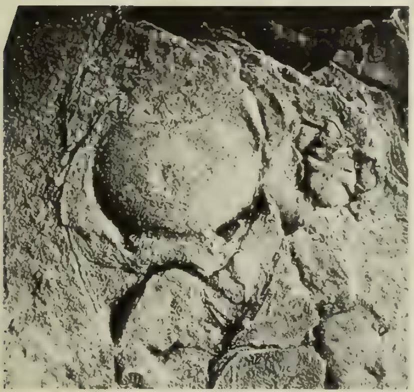
2



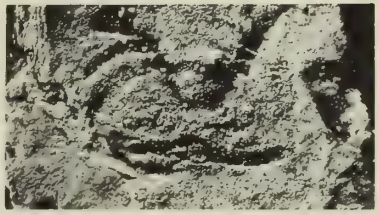
3



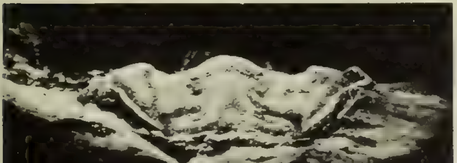
4



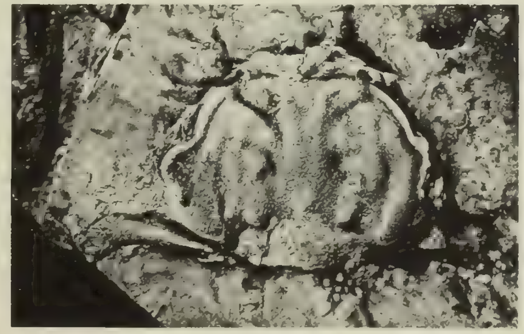
5



6



7



8

BRITISH MUSEUM
12 JUN 1967
NATURAL HISTORY

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

BURROWS AND SURFACE TRACES FROM THE LOWER CHALK OF SOUTHERN ENGLAND

W. J. KENNEDY

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 3
LONDON: 1967

BURROWS AND SURFACE TRACES FROM THE LOWER CHALK OF SOUTHERN ENGLAND

BRITISH MUSEUM
NATURAL HISTORY

BY

WILLIAM JAMES KENNEDY

Pp. 125–167; 9 *Plates*; 7 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 3
LONDON: 1967

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 15, *No.* 3 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation :
Bull. Br. Mus. nat. Hist. (Geol.).

© Trustees of the British Museum (Natural History) 1967

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 24 *November,* 1967 *Price* £2 2*s.*

BURROWS AND SURFACE TRACES FROM THE LOWER CHALK OF SOUTHERN ENGLAND

By WILLIAM JAMES KENNEDY

CONTENTS

		Page
I.	Introduction	127
II.	The trace fossils	130
III.	Location of specimens	131
IV.	Systematic descriptions	131
V.	Other burrows	156
VI.	Conclusions	161
VII.	Acknowledgments	162
VIII.	References	162

SYNOPSIS

The Lower Chalk of Southern England comprises between 17 and 80 m. of rhythmic alternations of more or less calcareous marly chalk. The whole sequence is intensely burrowed, the following burrow types are named: *Thalassinoides saxonicus* (Geinitz), *T.* cf. *suevicus* (Rieth), *T. ornatus* ichnosp. nov., *T. paradoxica* (Woodward), *Spongeliomorpha* sp., *Spongeliomorpha? annulatum* ichnosp. nov. and *Chondrites* sp. Several other forms are discussed, including " *Terebella* " *cancellata* Bather and *Keckia* (?) sp. Five burrow types too poor for detailed description are noted and discussed. Two other trace-fossils, " laminated structures ", regarded as related to *T. saxonicus* and *Pseudobilobites jefferiesi* ichnosp. nov. (the " problematicum " of Jefferies (1961, 1963)) are also described.

The Eocene form " *Terebella* " *harefieldensis* White is briefly discussed and interpreted as a crustacean boring. *Thalassinoides, Spongeliomorpha* " laminated structures ", *Pseudobilobites*, " *Terebella* " *cancellata* and two of the un-named burrows are regarded as the product of crustaceans, *Chondrites* and the other un-named burrows are attributed to " worms ".

Other trace fossils—borings and micro-coprolites-are also noted.

I. INTRODUCTION

(a) General Features. The Lower Chalk of Southern England comprises between 17 and 80 m. of marly blue or buff chalk, ranging in age from Lower to Upper Cenomanian. The present account is based chiefly on exposures along the North and South Downs, the Chilterns and the Isle of Wight, although sections to the north, at Hunstanton (Norfolk) and south-west (Dorset, Somerset and Devon) have also been examined.

Apart from the valuable coastal exposures, there are useful working sections around Lewes (Sussex), Burham and Holborough in the Medway Valley (Kent) and in the large pits at Barrington (Cambridgeshire), Houghton Regis and Totternhoe (Bedfordshire), Pitstone (Buckinghamshire), Chinnor and Childrey (Oxfordshire).

By far the best general account of the formation is still that given by Jukes-Browne (1903), whilst a brief outline of some of the depositional and post-depositional features has been given elsewhere (Kennedy, 1967).

In the Weald, Hampshire and the Chilterns, the base of the formation is generally marked by a sharp lithological break and a line of piping, the basal Glauconitic Marl being let down into the Gault or Upper Greensand below, generally without signs of marked erosion, and with occasional indications of continuous deposition from the Albian below. The basal few feet, rich in glauconite and phosphates, clearly indicates slow deposition; similar features appear occasionally in the lower part of the Chalk Marl above, as at Eastbourne (Sussex) and in the Isle of Wight. Above, the whole thickness can be interpreted as a sequence of rhythmic alternations of more and less calcareous (or marly) chalks, with carbonate contents varying between approximately 40% at the base, increasing upwards to 90–95% at the top of the Lower Chalk. Insoluble residue determinations suggest that these rhythms are visible when the difference in carbonate content is as low as 4–5%.

There is much variation in thickness of the " limestone " and " marl " members of rhythms, although in a general way, in the lower part the " marls " are 45–60 cm. thick, the " limestones " 15–30 cm. thick. In the middle part the alternations are 15–30 cm. thick, whilst in the upper part, there is great variation, made difficult to interpret by the low mud content which renders the alternations only faintly discernible. A general, although not invariable feature of these rhythms is that the " marl " to " limestone " contact is transitional, whilst the contact at the base of the marls is very sharp.

The following features indicate that the alternations are, at least in part, primary:

(i) The piping of " marls " into " limestones " and vice-versa, in a wide variety of burrows.

(ii) The occurrence of " limestone " pebbles, phosphatized, glauconitized and otherwise, in " marls ".

(iii) The cutting of " marl "–" limestone " junctions by erosion hollows.

Evidence of secondary segregation is suggested by the nodular appearance of some " limestones " and the occurrence of calcareous concretions in some of the " marls ". In addition, sponges, ammonites and other fossils in " limestones " are often undistorted whilst the same forms are crushed flat in " marls ", suggesting the pre-compactional deposition of carbonate in the more calcareous parts of rhythms.

The upper limit of the Lower Chalk in this region is marked by a sharp change in lithology at the base of the *plenus* Marls, associated in some areas with obvious signs of erosion, the sub-*plenus* erosion surface of Jefferies (1962, 1963).

Traced northwards, the Lower Chalk loses these features, thins considerably and in Norfolk at Hunstanton is clearly condensed, with signs of erosion at many levels. It rests, with a sharp break and obvious signs of erosion on the Red Chalk (Albian). The Chalk here is hard, and as pointed out by Peake & Hancock (1961) probably winnowed. These features, and a similar thinning and condensation in the underlying Albian suggest the presence of a stable massif in this region during part, at least, of the Cretaceous. The influence of this massif may, in part be responsible for the development, in the Chilterns and northwards, of the " gritty " phosphatic Totternhoe Stone (Middle Cenomanian).

Traced westwards, the Lower Chalk maintains its general features to the western limits of outcrop at Membury (S. Devon), where rhythms are still present in the chalky part of the sequence. Faunal evidence indicates that the base of the Chalk is diachronous in the south-west.

(b) THE CHALK. The general composition of the Chalk was first noted by Ehrenberg (Sorby 1861) and later by Sorby (1861), Hume (1893) and Jukes-Browne & Hill (1903, 1904). More recently Black (1953), Black & Barnes (1959) and Hancock (1963) have given additional information. The carbonate portion of the Chalk is now wholly calcite, and it is generally accepted that most was deposited as such, and that it is wholly biogenic in origin. The finer fractions are largely composed of coccoliths, both whole and fragmentary, whilst the coarser fractions consist of *Oligostegina*, foraminifera, sponge fragments, the broken-down prismatic layers of *Inoceramus* and echinoderm debris. Abundance of the latter gives rise to the " gritty " chalks such as the Totternhoe Stone and Melbourn Rock. The insoluble fraction, discussed previously by Hume (1893) and Hill (1903, 1904) includes, in addition to the clay fraction, detrital silt and sand grade quartz as the most obvious mineral, accompanied by authigenic glauconite, collophane and feldspar.

(c) BOTTOM CONDITIONS. Current activity is indicated by the presence at many levels of winnowed chalks and rolled, glauconitized and phosphatized pebbles and fossils. The body chambers of large ammonites are often full of small fossils, including ammonites up to 10 cm. in diameter, presumably swept in by bottom currents. Fragmentation of *Inoceramus* shells and echinoid tests may be due to current activity.

Intraformational conglomerates suggest local erosion, as do what appear to be large scour hollows, sometimes associated with large ammonites (Kennedy, 1967).

The presence of burrowing bivalves such as *Pholadomya*, *Cucullaea*, and *Panopea* suggest soft bottoms, as does the presence of *Teredina amphisbaena* (Goldfuss), a form which I have never seen associated with wood (although *Teredo* bored wood occurs). Like the recent *Teredo* (*Furcella*) *polythalamia* (Linné) (Oosting 1925) this form appears to have lived in mud. Although soft, the bottoms must have been in the form of a stiff mud, since the small solitary corals and serpulids which are so common would not survive in a fluid mud, nor would larger epifaunal forms such as the limid and pectinid bivalves and *Inoceramus*, the latter possibly byssally attached to the sea floor. Equally, the lobster-like crustacean *Enoploclytia* presumably needed a firm bottom to walk across. Intense burrowing suggests bottoms rich in organic debris.

There is little evidence of rock bottoms (hardgrounds) in the Lower Chalk, erosion surfaces, when they occur, lacking the epifauna of bryozoa, serpulids and cemented bivalves present on the Chalk Rock hardgrounds. Borings in, and epifaunas on, the phosphatized top of the Upper Greensand in the south-west indicate hard bottoms here at least.

(d) DEPTH OF DEPOSITION. The abundance of coccoliths suggests deposition below the upper limit of present day coccolith abundance (60 m.): study of the sponges indicates a depth of 280 m. (Cayeux 1897: Turonian–Senonian) or 300 m. (Gignoux 1926: Campanian). Since it is generally agreed that the Chalk Marl, like the Chalk Rock (U. Turonian) represents shallower conditions than the rest of the Chalk (Jukes-Browne & Hill 1904), a depth lower than the maximum is implied for this part of the Lower Chalk. Burnaby (1962) has discussed depth variation in the Lower Chalk sea, on the basis of the foraminifera.

II. THE TRACE FOSSILS

Two types of trace fossil are described from the Lower Chalk; burrows and surface traces. Of these, burrows are by far the most important, and are one of the most prominent features of the sediment (Pls. 1, 2).

(a) Burrows. In modern marine environments a great variety of organisms utilize the region below the sediment–water interface for refuge, nourishment and habitation. Arthropods, echinoderms, molluscs, coelenterates, many groups of worms (particularly annelids) are amongst the most important groups of invertebrates, whilst many higher animals burrow. In addition, the interstitial fluid between sedimentary particles supports a large fauna and flora (Purdy, 1964). Particles of sediment themselves have a coating of bacteria, utilized by detritus feeders; total content increasing as particle sizes decrease (Newell 1965).

The influence of these organisms on the sediment is considerable. Davidson (1891) described the activities of lobworms in the Holy Island Sands, between Holy Island and the Northumberland coast, suggesting nearly two thousand tons of sand was ingested per acre per annum, and that the top 60 cm. of sediment passed through the worms' bodies every 22 months. Taylor (1964) quotes data suggesting 80–90% of the sands in the Bermudas is made up of ground shell matter that has passed through the intestinal tracts of echinoderms. Both indicate the importance of biological destruction of sedimentary structures. Local topography can be influenced by burrowing organisms; the hummocky bottom topography of the Bahaman platforms is attributed to organic activity (Taylor 1964), whilst erosion of callianassid burrows produces the characteristic sand-pipe topography of some intertidal regions (Weimer & Hoyt 1964). Many of the problematic mounds and depressions seen in deep-sea photographs are probably organic in origin.

Many burrows are lined with mucus, whilst *Callianassa major* Say lines its burrow with collophane-cemented sand pellets (Weimer & Hoyt 1964). Many sediment eaters form durable faecal pellets (Moore 1939). These features indicate the importance of burrowing organisms in stabilization and aggregation of sediments.

Taylor (1964) has pointed out the chemical effects of bottom dwelling organisms on both Eh and pH, particularly where the release of organic and inorganic acids is concerned, suggesting great importance in diagenesis at the early burial stage.

Burrowers are also responsible for the creation of refuges for many commensals. The burrow of the worm *Urechis*, for instance, is inhabited by a gobie, polynoid worm and pinnotherid crab (Fisher & MacGinitie 1928). Dales (1957) gives details of similar associations in other burrowing organisms.

(b) Burrows in the Lower Chalk. The whole of the Lower Chalk studied is intensely burrowed (Pl. 2, figs. 2–4), often many times over (Pl. 2, fig. 4). In general, these structures can be studied in section only, in the form of sedimentary mottling.

Only rarely can the pattern and form of systems be made out. Burrowing, often equally intense to that in the Lower Chalk, can be seen, in suitable lithologies, in the overlying Middle and Upper Chalk.

Simpson (1957), Häntzschel (1962) and Seilacher (1964) have discussed the various conditions of preservation of trace fossils; in the Lower Chalk the following modes of preservation of burrows can be distinguished:

(i) Differences in composition and colour of burrow filling and matrix.
(ii) Pyritization (an example of a pyritized burrow, overgrown by a pyrite nodule was figured by Mantell (1822, pl. 16, fig. 16)).
(iii) Coating of the outer surface of the burrow by iron sulphide (often altered to Limonite), perhaps influenced by the former presence of a mucus lining.

Burrowing in the English chalk has been mentioned only briefly by previous authors, generally as " mottling " or " piping ", or by reference to them as sponges (Webster 1814) or " Zoophytes " (Taylor 1823). More recently, Wood (1965), discussing the Lower Chalk at Dover, mentions " extensive reworking " by " bottom living organisms, the infilling of the burrow traces being a lighter colour than the main mass of the sediment ".

The only previous work on trace-fossils from the Lower Chalk is that of Davies (1879) and Bather (1911). The terebellids described by these authors are, in part, burrows, whilst the latter described a single fragment referred to as *Keckia* (?) sp.

III. LOCATION OF SPECIMENS

The author's collection and the types of " *Terebella* " *cancellata* Bather and " *T.*" *harefieldensis* White are in the collections of the British Museum (Natural History), Dr. R. P. S. Jefferies' collection is in the Sedgwick Museum, Cambridge. These are abbreviated to B.M. (N.H.), and S.M.C. respectively in the following account.

IV. SYSTEMATIC DESCRIPTIONS

Ichnogenus ***THALASSINOIDES*** Ehrenberg 1944

TYPE SPECIES. By the original designation of Ehrenberg (1944) *Thalassinoides callianassae* Ehrenberg, from the Miocene (Burdigalian) of Burgschleinitz, Eggenberg, Austria.

DISCUSSION. This trace fossil genus was erected for a ramifying system of cylindrical burrows from Miocene sands, intimately associated with, and probably formed by crustaceans (identified as *Callianassa* sp.) described by Ehrenberg six years previously (1938). The original diagnosis is as follows: " Die Gattung ,,*Thalassinoides* " wäre wie folgt zu kennzeichnen: Gänge und Gangsysteme oder bzw. deren Ausfüllungen (Kerne) mit mehr oder weniger Y-förmigen Gabelungen oder Verzweigungen, meist ohne wesentliche Oberflächenskulpturen: sonstige Form und Durchmesser merklich wechselnd.

"Typus-,, Art " Th. *callianassae* mit den Charakteren der ,, Gattung " aus dem Burdigal von Burgschleinitz bei Eggenberg. N : D. Typusexemplar das im Paläontolog. u. Paläobiolog. Institut der Universitat Wien verwahrte Urstück zu Ehrenberg 1938 Tafel 28,5."

A brief diagnosis in English has been given by Häntzschel (1962). On the basis of the present material it may be emended as follows:

Extensive burrow systems with both vertical and horizontal elements. Burrows cylindrical, between 2 and 20 cm. in diameter. Branching regular, characterized by Y-shaped bifurcations, swollen at point of branching. Horizontal elements joining to form polygons. Burrow dimensions variable within a system. Horizontal systems connecting to surface by vertical or steeply inclined shafts, widely associated with callianassid remains.

Häntzschel (1962, 1965) regards *Vomacispongites* de Laubenfels (1955 : 108) as a synonym of *Thalassinoides*. *Vomacispongites* was introduced by de Laubenfels as an " unrecognizable supposed sponge ", as follows:

" *Vomacispongites* de Laub. nom. nov. (pro *Spongites* Schloth. 1820 (non. Oken 1814)) ", the type species is *Spongites pertusus* Schlotheim (1820 : 369) based on a specimen from a Cretaceous chert from Amberg (W. Germany), compared by von Schlotheim to *Spongia pertusa* Esper (Esper 1799 : 246–7, pl. 26, figs. 1, 2). Esper's figure is clearly a sponge, and I can only presume that Häntzschel has examined the original specimen, since the original description does not suggest a *Thalassinoides*. The genus *Aschemonia* Dettmer (1914) is too poorly defined for comparison, but may well be a *Thalassinoides*.

In addition to the association of *Thalassinoides* with *Callianassa* sp. recorded by Ehrenberg (1938), Glaessner (1947) describes what are clearly *Thalassinoides* in association with callianassids from the Eocene of Victoria (Australia), whilst Mertin (1941) records *Protocallianassa* in association with what are probably *Thalassinoides* in the Upper Cretaceous of Germany. Häntzschel (1965), Seilacher (1955, 1964), Farrow (1966) and Hallam (1961) all regard *Thalassinoides* as a crustacean burrow.

Thalassinoides is very widespread, and has been recorded from the Trias (Reis 1910, Fiege 1944), Lias (Rieth 1932, Seilacher 1955, Hallam 1961), Oxfordian (Wilson 1949), Portlandian (Pruvost & Pringle 1924, Arkell 1935), Cretaceous (Geinitz 1842 etc.) and Tertiary (Ehrenberg 1938, Glaessner 1947). The geographical range of this form covers Europe, Asia and Australia.

In Britain, this trace fossil has been recorded from the Lower Lias by Hallam (1961), whilst the fucoids recorded by Blake & Hudleston (1877 : 271) and Arkell (1936 : 63) from the Oxfordian (Corallian, Nothe Grits) of the Dorset coast, and figured from a similar horizon in Yorkshire by Wilson (1949 : 256, pl. 10) are clearly *Thalassinoides*, as are the fucoids figured by Arkell (1925 : pl. 22, *a*) from the Portlandian (Portland Sand, Black Sandstones) of the Dorset coast. Farrow (1966) records it from many levels in the Yorkshire Jurassic.

I have noted this trace fossil at many horizons and localities: Triassic: Rhaetic, South-Devon coast between Seaton and Lyme Regis, piping the basal bone bed into the underlying Keuper (Text-fig. 2, G.). Jurassic: The whole of the Dorset Lias (Text-figs. 1, G–J; 2, F). Cretaceous: Lower Greensand, Folkestone beds at Folkestone (Text-fig. 2, I–K) associated with *Gyrolithes* type structures; Upper Greensand of Southern England and throughout the whole of the Lower Chalk and in the Middle

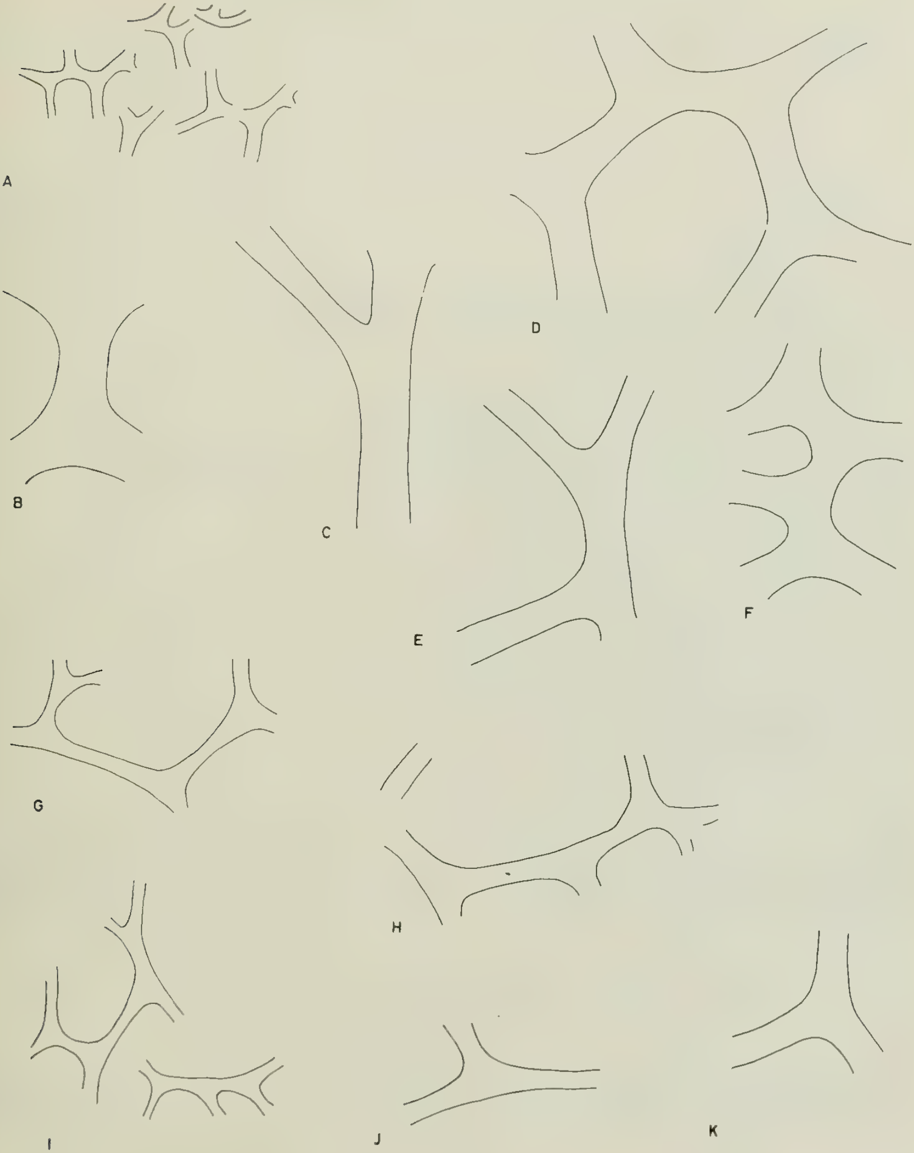


Fig. 1. A. *Thalassinoides* sp. Lower Chalk, ?Upper Cenomanian; White Nothe, Dorset. Plan, $\times \frac{1}{16}$. B, C. *Thalassinoides saxonicus* (Geinitz). Lower Chalk, Middle Cenomanian, Chalk below Totternhoe Stone; Houghton Regis, near Dunstable, Beds. Plan, $\times \frac{1}{16}$. D, F. Laminated structures. Lower Chalk, Middle Cenomanian; near Beachy Head, Eastbourne, Sussex, Plan, $\times \frac{1}{16}$. E. Laminated structure. Lower Chalk, Middle Cenomanian, bed 7; Folkestone, Kent. Plan, $\times \frac{1}{16}$. G–J. *Thalassinoides* sp. Upper Lias, Toarcian; near Seatown, Dorset. Plan, $\times \frac{1}{16}$. K. *Thalassinoides* sp. Upper Greensand; Foxmould, Humble Point, South Devon. Plan, $\times \frac{1}{16}$.

and Upper Chalk where burrows are preserved (i.e. the Melbourn Rock (Lower Turonian) and below the Chalk Rock (Upper Turonian)). At least four forms can be recognized in the Lower Chalk.

Thalassinoides saxonicus (Geinitz)

(Pl. 1, fig. 1; Pl. 5, figs. 2, 3; Pl. 6, figs. 3, 4; Text-figs. 1, B, C; 2, E)

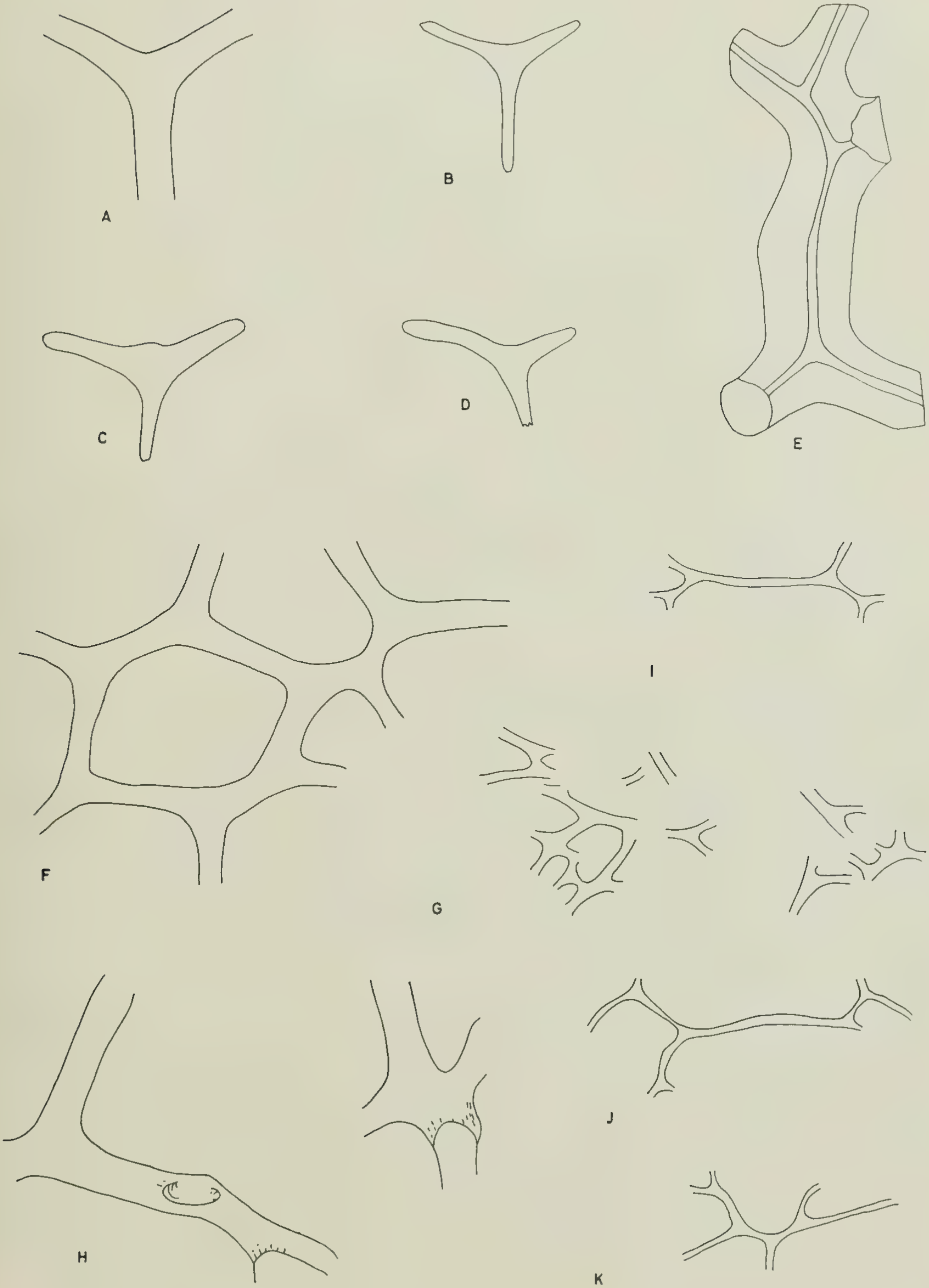
1842 *Spongites saxonicus* Geinitz : 96, pl. 12, fig. 1 only (fig. 2 = *Ophiomorpha nodosa* Lundgren).
1852 *Spongites saxonicus* Geinitz; von Otto : 20, pl. 6, figs. 2, 3.
1871 *Spongites saxonicus* Geinitz; Geinitz : 21, pl. 1, figs. 1–5 only.
1878 *Spongia saxonica* Geinitz; Frič : 149.
1878 *Spongites gigas* Frič: 75, 149.
1885 *Spongites saxonicus* Geinitz; Počta : 30.
1899 *Spongites saxonicus* Geinitz; Semenow : 6.
1909 *Cylindrites spongioides* Goeppert emend. Richter : 8, 11.
1912 *Spongites saxonicus* Geinitz; Dettmer : 114–126 (pars.), ?pl. 8, figs. 4–6.
?1914 *Aschemonia gigantea* Dettmer : 287, fig.
1915 *Spongites saxonicus* Geinitz; Dettmer : 285–287 (pars.).
?1928 *Spongites* sp. Lamprecht : 8, 9, pl. 2.
1932 *Spongites saxonicus* Geinitz; Rieth : 30, pl. 5*a*, 1, 2.
1934 *Spongites saxonicus* Geinitz; Andert : 68.
1934 *Spongites saxonicus* Geinitz; Häntzschel : 313.
1944 *Spongites saxonicus* Geinitz; Fiege : 419.
1952 *Spongites saxonicus* Geinitz; Häntzschel : 146.
1954 *Cylindrites saxonicus* Prescher : 59, text-fig. 19.
?1955 *Spongites* sp., Seilacher : text-fig. 5, 98.
1962 *Spongites saxonicus* Geinitz; Häntzschel : 218.
1965 *Spongites saxonicus* Geinitz; Häntzschel : 88.
1967 "*Spongites*" *saxonicus* Geinitz; Kennedy : 368

DIAGNOSIS. *Thalassinoides* with horizontal tunnels between 5 and 20 cm. in horizontal diameter. System very extensive, tunnels joining to form huge polygons up to 60 cm. across, connected to surface by short vertical shafts. Surface of burrow mamillated, individual mounds 5 to 10 mm. long, elongated parallel to length of tunnel.

LECTOTYPE. Here designated, the original of *Spongites saxonicus* Geinitz 1842, pl. 22, fig. 1 only: Upper Cretaceous; Germany.

DESCRIPTION. Systems arise from short, vertical shafts, equal in diameter to the widest part of the horizontal elements, which are up to 40 cm. below the surface. The horizontal tunnels are elliptical in section and at a single level. Tunnel diameters

FIG. 2. A–D. *Thalassinoides visurgiae* Fiege (after Fiege 1944) × $\frac{1}{8}$. E. *Spongites saxonicus* Geinitz, Sketch of lectotype (after Geinitz 1842) × $\frac{1}{4}$. F. *Thalassinoides* sp. Lower Lias; Pinhay Bay, S. Devon. Plan, × $\frac{1}{16}$. G. *Thalassinoides* sp. Top of Keuper, full of Rhaetic Bone Bed; Charlton Bay, S. Devon. Plan, × $\frac{1}{8}$. H. *Thalassinoides* sp. Upper Chalk, Upper Turonian, Chalk Rock; Hitch Wood, near Hitchin, Herts. Plan view of 3-dimensional tunnel system beneath the Chalk Rock hardground. × $\frac{1}{4}$. I–K. *Thalassinoides* sp. Lower Greensand, Folkestone Beds, Lower Albian; Copt Point, Folkestone, Kent. Plan, × $\frac{1}{16}$.


A
B
E
C
D
F
I
G
H
J
K

vary between 20 by 13 cm. in the centre of systems, to 5 by 3·5 cm. at the extremities. Branching is very regular, at intervals of about 30 cm. tunnels bifurcate, with a symmetrical Y-shaped junction, slight widening giving rounded angles. The overall pattern is of large polygons up to 60 cm. across (Plate 1, fig. 1). Specimens showing terminations are uncommon; the ending figured (Plate 5, fig. 2) is swollen, measuring 12 by 5 by 3·5 cm. at the end of a 3 by 2·5 cm. tunnel. The outer surfaces of tunnels are covered by low mounds: on small specimens these vary from 17·5 to 18 mm. long by 7·5 to 11·5 mm. wide by 3·5 to 6·5 mm. high: on larger specimens 16–18 mm. by 9–12 mm. by 4–6 mm. The arrangement of these mounds shows little regularity other than a preferred orientation parallel to the length of the tunnel. These structures are rarely preserved on bottom surfaces, which are covered by a felted mass of *Chondrites* burrows (Pl. 5, fig. 3).

Sections of tunnels suggest that some of these mounds are discrete, with a definite separation from the burrow filling. The majority have only a suggestion of a plane of separation. In addition to mounds, oval depressions of a similar size, surrounded by a raised rim are present, as are ridges, generally 20 mm. long and 2 mm. high, running between the mounds.

Discussion. The lectotype, as figured by Geinitz, is a large, branching cylindrical body with a maximum diameter of 5 cm. The surface is covered by small mounds, 5 mm. long and 2 to 3 mm. wide, elongated parallel to the length of the branches. A smooth half cylinder 5 mm. in diameter runs along the centre of the main part, joining with similar bodies on the branches (Text-fig. 2, E). The other specimen figured by Geinitz (pl. 22, fig. 2) can clearly be referred to *Ophiomorpha nodosa* Lundgren.

Geinitz regarded *Spongites saxonicus* as a horny sponge (Ceratospongidae), a view also held by von Otto (1854), Frič (1878), Počta (1885) and many other early workers. Goeppert (1842 : 115, pl. 46, figs. 1–5, pl. 48, figs. 1, 2) described what he regarded as a fossil alga, *Cylindrites spongioides*, and he subsequently (1847) considered this species to have priority over *S. saxonicus*, and that both were algae. *Cylindrites spongioides*, as originally proposed, includes a number of different trace-fossils. Forms figured on plate 46, figs. 1–4 are simple crustacean burrows (type B, p. 47), or possibly *Ophiomorpha*. The other specimens (pl. 46, fig. 4; pl. 48, figs. 1, 2) are smooth cylindrical burrows with swollen portions, differing from *S. saxonicus* in smaller size and lack of ornament.

Cylindrites has been used by many authors for fucoids (Eichwald 1865, Watelet 1866 etc.) or trace fossils (Prescher 1954), but is not available due to prior usage by Gmelin (1793) and Sowerby (1825) as gastropod genera. Richter's (1909) emendation of *Cylindrites* is unfortunate, for he clearly includes large burrows (up to 15 cm. in diameter), probably *Thalassinoides saxonicus*, specimens of *Ophiomorpha nodosa* (pl. 9, fig. 7, pl. 12, fig. 5, pl. 13, fig. 6), plant debris (pl. 12, figs. 1, 2, pl. 13, fig. 6) and smooth burrows with swollen portions (pl. 9, figs. 1–2).

As pointed out by Häntzschel (1952), *Cylindrites spongioides* may be a synonym of *Halymenites cylindricus* Sternberg:

" H. fronde fistulosa terente pinnatim ramosa, ramus opposites simplicibus patenibus cylindricus obtusis, terminale longiors . . . In schisto saxi arenaci Pirnensis (Greensand anglorum) prope Tetschen ad albim Bohemae." (Sternberg 1833.)

Until the branching pattern of *C. spongioides* is described, it is not possible to decide if it is a form of *Thalassinoides*, although it is clear that it is a smooth crustacean burrow, the swollen portions representing " turn-arounds ", comparable to the burrows produced by the living crustaceans *Upobegia pugettensis* (Dana) (MacGinitie 1930) and *Callianassa californiensis* Dana (MacGinitie 1934, Stevens 1928). These burrows were noted as early as 1760 by Schulze (41–46, pl. 2, figs. 1–5) who regarded them as crinoid remains. In view of their interpretation as callianassid burrows it is interesting to note that Goeppert (1854) recorded *C. spongioides* in association with remains of *Protocallianassa antiquua* (von Otto).

Dettmer (1912) regarded *Spongites saxonicus* as a giant foraminiferan!

Häntzschel (1934, 1935) records *Xenohelix saxonica* Häntzschel (=*Gyrolithes* Saporta) associated with *Spongites saxonicus*; spiral structures, perhaps *Gyrolithes* occur in the Folkestone beds (L. Albian) at Folkestone, Kent in association with *Thalassinoides*, and have been recorded associated with *Ophiomorpha* in the Miocene of Borneo (Keij 1965) and elsewhere (Kilpper 1962). This type of association indicates the artificial nature of trace-fossil taxa, as it suggests that *Gyrolithes*, *Thalassinoides* and *Ophiomorpha* are all synonymous, the first having priority.

The best preserved examples of *T. saxonicus* I have found are from beneath the Totternhoe Stone (Middle Cenomanian) of the Chilterns, particularly Houghton Regis (Bedfordshire). Here, hard, gritty Totternhoe Stone is piped into the very soft chalk below and the burrows so filled can be completely freed of matrix (Pl. 5, figs. 2, 3; Pl. 6, figs. 3, 4).

The presence of phosphatic pebbles and shells in these burrows indicates that they were open on the sea floor, and were filled passively, probably after being vacated. Individual systems extend over several square metres and indicate firm sediment, as I have never seen signs of collapse into them.

The ridges on the outer surface are interpreted as scratches produced by the inhabitant whilst digging or moving through the system; the mamillated surface as a result of worked pellets pushed into the wall of the tunnel and smoothed off or worn smooth by the passage of the animal's body. Pellets are impressed into burrow walls in this manner by the crustacean *Callianassa major* Say (MacGinitie *in* Häntzschel 1952, Weimer & Hoyt 1964). The oval depressions with their surrounding ridges appear to be the sites of pellets of soft chalk which have been washed away in preparation. The most likely purpose of these pellets is to support the burrow walls, a procedure used by living callianassids (Pohl 1946); swollen portions at points of branching and burrow terminations are comparable with the " turn arounds " of burrows of this group (MacGinitie 1930, 1934, Pohl 1946). All the features of *T. saxonicus* are thus comparable with Recent callianassid burrows. This view is enhanced by the presence, in the infilling of *T. saxonicus*, of rod-like phosphatized faecal pellets (type A of Wilcox 1953), more abundant than elsewhere in the Lower Chalk, which, from the presence of internal canals, are diagnostic of anomurans (Wilcox 1953, Moore 1932).

Internally, these burrows show intense re-working (see p. 149). A puzzling feature of previously described specimens of *T. saxonicus* is the small burrow running down the centre of the lower surface of the system. In the lectotype this is very regular, but in other specimens it clearly strays from the mid-line. Geinitz (1842) interpreted this as a juvenile sponge. My own material suggests that this is another, smaller species of *Thalassinoides*, which sometimes follows the mid-line of the bottom of the larger burrow, but which often leaves, passing out into the surrounding sediment (Pl. 6, fig. 4). These smaller burrows may be the products of the juveniles of the *T. saxonicus* animal, but as I have never seen transitions it is regarded as a distinct form, *T. ornatus* nov. (p. 141).

Whilst most systems correspond to the above description, occasionally tunnels are found filled with coarse, sandy chalk made up of shell fragments and microfossils. This material represents the remains of the burrow filling after the inhabitant has sifted out the finer portion for ingestion; the faecal pellets associated with these burrows show only fine-grained material when sectioned (Wilcox 1953), suggesting this mode of feeding. Presumably the coarser debris was normally removed from the system and washed away by bottom currents, being only occasionally packed into a disused part of the burrow. In a single instance, from the Upper Cenomanian at Dover, a large mass of this coarse debris, lying above a *T. saxonicus* system seemed to represent material dumped outside the burrow opening adjoining the entrance shaft.

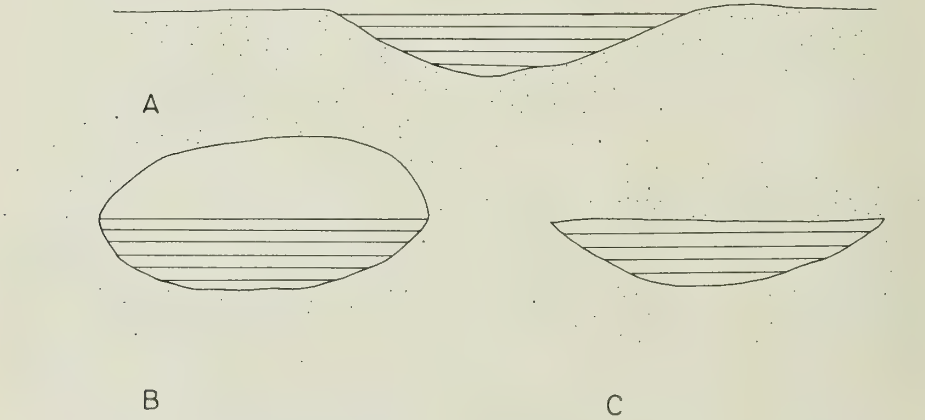


Fig. 3. Alternative interpretations of laminated structures. A. As surface trace; B. As partially filled burrow; C. As totally filled burrow with semi-circular section. All ×¼.

Thalassinoides saxonicus and "Laminated structures". I have used the name "laminated structures" (Kennedy 1967) for problematic structures occurring throughout the Lower Chalk which, in section, show fine, horizontal laminations made prominent by their resistance to weathering (due to a calcite cement) and brown colour (due to disseminated limonite). In plan, these structures show a form identical in size-range and mode of branching with *T. saxonicus* (Text-fig. 1, D–F). In section they can be described in terms of a continuous series defined by two end members:

(i) Horizontal bands, up to 60 cm. long and 5–10 cm. deep, laminated throughout, the laminations essentially parallel.

(ii) Semi-circular sections, the curved surface downwards, with diameters from 10 cm. upwards. With increasing diameter the radius of curvature of the lower surface increases, passing into form (i). Laminations are essentially parallel, with a tendency to dip towards the centre of the section.

In both cases, weathered and cut sections show that the laminations consist of alternations of normal chalk and coarse debris of shell and echinoderm fragments, foraminifera and other sand grade microfossils, cemented by calcite and coloured brown by small quantities of limonite, perhaps after pyrite. The laminations are between 2 and 20 mm. thick, and may vary laterally (Pl. 8, fig. 3). In thin section, these structures show very ill-defined graded bedding, the coarse material grading up into the normal chalk above.

These laminated structures are cut by burrows (Pl. 8, fig. 3; Pl. 5, fig. 1) indicating a primary origin. Whilst the general sense of the laminations is horizontal and parallel, corrugations and other disturbances are common (Pl. 8, fig. 3). Some of these structures are clearly the result of subsequent burrowing (Pl. 8, fig. 3), whilst other irregularities appear to be the result of slumping of the layers (Pl. 8, fig. 3). Bottom surfaces are rather irregular (Pl. 8, fig. 3), in part as a result of burrows along the basal interface.

Interpretation. In view of the similarity in size-range of these structures and *Thalassinoides saxonicus* and the identical branching pattern, they are clearly the result of the activities of the same organisms; crustaceans. Whereas *T. saxonicus* is clearly a burrow, elliptical in section, laminated structures generally have a flat top. Three interpretations are possible (Text-fig. 3).

(i) They are the filling of the lower parts of burrows.
(ii) They are completely filled burrows semi-circular in section.
(iii) They are a surface trace.

I have examined many examples in the field; most show no indications of an associated burrow. A few show what could be interpreted as the upper part of a burrow, but at present the evidence suggests they were a surface trace, although the relationship seen in Plate 8 could be interpreted as the intersection of two burrows with a semicircular section, completely full of laminated sediment.

The laminations are interpreted as the result of sifting of the sediment by the animals producing these structures. As already indicated (p. 137) faecal material suggests they lived on the finer fractions; the coarse layers are the remains left after this sifting. Whilst this can explain the formation of one layer, I can offer no explanation of the repeated alternation of coarse and fine layers.

Explanation of these structures as a feeding trace of *Teichichnus* type (Seilacher 1955, Häntzschel 1962) is unsatisfactory due to the absence of an obvious burrow in association, unless the initial burrow were very shallow and invariably broke the sediment-water interface. An inorganic origin—that these are *Thalassinoides*, exposed by erosion and filled by swept-in coarse material alternating with fine mud deposited by gravitational settling or other currents—is rejected; other hollows on the sea floor lack a laminated fill, whilst one would expect to find truncated *Thalassinoides* without a laminated fill, which I have never seen.

Occurrence. Solid specimens of *T. saxonicus* occur abundantly beneath the Totternhoe Stone in the Chilterns. Large *Thalassinoides*, identical in size and mode of branching are common in all coastal sections whilst large oval burrow sections are abundant in all sections and are regarded as identical with *T. saxonicus*. A large species of *Thalassinoides* occurs beneath the Chalk Rock (Text-fig. 2, H) but differs from *T. saxonicus* in having three-dimensional tunnels. These were described by Billinghurst (1927) as " solution channels ".

T. saxonicus is widely recorded from the Cretaceous of Germany and Central Europe. The specimen of *Thalassinoides* figured by Seilacher (1955) from the Tertiary may belong to this form. " Laminated structures " are common throughout the whole of the Lower Chalk, particularly in the Middle Cenomanian. At Folkestone (Kent) bed 7 (Jukes-Browne & Hill 1903) can be traced all along the coast, even when high in the cliffs, because of the abundance of these structures.

Thalassinoides cf. ***suevicus*** (Rieth)

(Pl. 1, fig. 2)

1932 *Spongites suevicus quenstedti* Rieth : 274.
1932 *Spongites suevicus* Quenstedt; Rieth : 292.
1932 *Cylindrites suevicus* (Quenstedt) Rieth, pl. 13*a*, *b*.
?1944 *Thalassinoides visurgiae* Fiege : 416–421, 424, text-fig. 4.
1955 *Spongites suevicus* Quenstedt; Seilacher, text-figs. 5, 57.
?1964 *Thalassinoides* sp. Häntzschel : 302, pl. 14, fig. 3.
1964 *Thalassinoides suevicus* (Rieth); Häntzschel : 302.

A *Thalassinoides* with tunnel diameters between 2 and 5 cm. is occasionally seen in fallen blocks of Upper Greensand and Lower Chalk at many coastal sections (Eastbourne, Compton Bay, etc.). Those in the Upper Greensand in part arise from the base of the Glauconitic Marl.

In size, mode and angle of branching these are comparable with " *Spongites* " *suevicus* Rieth, from the Lias and Dogger of Germany (as pointed out by Häntzschel (1964 : 302) this name must be attributed to Rieth). There is also a strong resemblance to the fragment figured by Häntzschel (1964) from the Campanian of Beckum (Westphalia).

Thalassinoides visurgiae Fiege, from the Trias (Muschelkalk) of North Germany, is based on branching portions (Text-fig. 2, A–D) and appears identical with *T. suevicus*.

T. cf. suevicus differs from *T. saxonicus* in its much smaller size and absence of ornamentation. It is not referred definitely to *T. suevicus* because of the poor preservation. The systems are horizontal as far as has been seen. It is not clear how much of the piping beneath the Glauconitic Marl is due to this form (Pl. 1, fig. 3), but attitude and tunnel diameters are comparable.

Specimens of *Thalassinoides* from the Upper Greensand and from beneath the

Totternhoe Stone at Hunstanton, agreeing in size with this form occasionally show internal structure, seen in section as concavo-convex laminations (Text-fig. 6, D).

This type of burrow filling is discussed on page 161.

OCCURRENCE. Fairly frequent in the whole of the Lower Chalk of southern England. Comparable forms occur in the Lias and Upper Greensand: Lias and Dogger of Germany and Campanian of Bochum, Germany.

Thalassinoides ornatus ichnosp. nov.

(Pl. 6, fig. 4; Pl. 7, fig. 6)

DIAGNOSIS. Small *Thalassinoides*, tunnel diameters between 16 by 8 mm. and 22 by 10 mm. System largely horizontal, surface of tunnels covered in reticulate ridges.

HOLOTYPE. B.M. (N.H.) T.559. Paratype B.M. (N.H.) T.551.

LOCALITY AND HORIZON. The holotype (associated with *T. saxonicus*) is from the Lower Chalk immediately beneath the Totternhoe Stone at Houghton Regis (Bedford shire) (National Grid Reference T.L.013233) and is Middle Cenomanian in age. The paratype is from the same horizon and locality. This species is not uncommon beneath the Totternhoe Stone elsewhere in the Chilterns: poorly preserved material from the Lower Chalk of the Weald may also belong to this form.

DESCRIPTION. The tunnels are generally horizontal or gently inclined, with typical *Thalassinoides* branching pattern. Individual tunnels are oval in section, dimensions varying between 16 by 8 mm. to 22 by 10 mm. The whole surface is covered in delicate intersecting ridges (Pl. 7, fig. 6); some tunnels are gently curved. Branching points are swollen, whilst swollen portions with diameters of about three times that of the adjoining tunnel are present.

DISCUSSION. This form is quite common beneath the Totternhoe Stone in Bedfordshire, often following the mid-line of the lower surface of *T. saxonicus* burrows (Pl. 6, fig. 3). As already suggested (p. 138) this may be the explanation of the cylindrical central body figured by previous workers (Geinitz 1842, 1871, von Otto 1854, Seilacher 1955 etc.). This pattern is not regular, the smaller burrows often passing through the larger burrows and occurring in the surrounding sediment.

Interpretation of *T. ornatus* as the work of juveniles of *T. saxonicus* is considered unlikely in the absence of intermediate forms.

As with the forms of *Thalassinoides* already discussed, the features of *T. ornatus* agree with an interpretation as crustacean burrows: reticulate surface ridges are scratches on the inside of the burrow produced during digging or when moving through the system, the swollen portions are clearly " turn-arounds ".

The surface ornament of *T. ornatus* resembles that on *Spongeliomorpha* (p. 151), also regarded as a crustacean burrow. The two forms are distinguished by the more regular ornamentation and branching of *T. ornatus*. This form differs from *T.* cf. *suevicus* by the presence of a reticulate ornamentation and swollen " turn-arounds ". Clearly, with poorly preserved material the two forms may be confused.

Thalassinoides paradoxica (Woodward)

(Pl. 3; Pl. 4; Pl. 8, fig. 5; Pl. 9, fig. 2; Text-figs. 4, 5, A–B)

1814 . . . singular organic body . . ., Webster, pl. 27, fig. 1.
1823 . . . a remarkable ramifying zoophyte . . ., Taylor : 82.
1830 *Spongia paradoxica* Woodward : 5.
1833 *Spongia paradoxica* Woodward; Woodward : 29, 30, 54.
1835 . . . a ramose zoophyte . . . Rose : 54, 275, 276.
1859 *Spongia paradoxica* Woodward; Wiltshire : 275, 277, pl. 1, figs. 1, 2.
1864 *Spongia paradoxica* Woodward; Seeley : 331.
1869 *Siphonia paradoxica* (Woodward) Wiltshire : 176.
1871 Problematicum, Geinitz, pl. 38, fig. 8.
1884 *Spongia paradoxica* Woodward; Hughes : 273–279.
1899 *Spongia paradoxica* Woodward; Whitaker & Jukes-Browne : 36, 55.
1900 *Spongia paradoxica* Woodward; Jukes-Browne & Hill : 303.
1903 . . . stems of *Siphonia* . . . , Jukes-Browne & Hill : 209.
1932 Problematicum, Rieth, text-fig. 35 (after Geinitz).
1961 "*Spongia paradoxica*" Woodward; Peake & Hancock : 301, 330.
?1961 "*Spongia paradoxica*" Woodward; Rios & Hancock, pl. 16.
1962 *Spongia paradoxica* Woodward; Häntzschel : W 242.

DIAGNOSIS. Medium sized *Thalassinoides*, with irregular, very extensive horizontal burrow network, occurring at several levels, connected by vertical shafts. Diameter of tunnels variable, between 7 and 60 mm., short blind tunnels very common. Surface covered with longitudinal ridges. Generally occurs associated with erosion surfaces.

NEOTYPE. Here designated, B.M. (N.H.) T.545 from the *Paradoxica* bed, base of Lower Chalk (Lower Cenomanian); Hunstanton Cliff, Hunstanton, Norfolk.

DESCRIPTION. This is the most irregularly branching *Thalassinoides* I have seen. The burrows have an irregular section, and may be depressed or rounded-angular, varying in a single system between 7 and 60 mm. in diameter. A large tunnel may give rise to a side branch less than a quarter of its own diameter. As in other species of *Thalassinoides*, the principal element of branching is a Y fork, with an increase in diameter around the point of branching, the tunnel tending to widen between the forks of the Y. Distance between branching points is very variable, between 1 and 20 cm. Many of the branches terminate after short distances, giving the system an antler-like appearance, whilst at every point on the system there are small blunt protuberances varying from a few millimeters to several centimetres long, representing abandoned or unfinished tunnels. Even smaller knobs are also present. Where several branches occur close together the tunnels may widen to form a flat chamber (Pl. 8, fig. 5) up to 10 cm. long and 5 cm. wide with five or six tunnels leading off.

The most striking feature of the branching pattern is that the Y-forks occur in three dimensions, whilst most of the elements of the system are horizontal, joining into small irregular polygons (Text-figs. 4, 5, A–B). An individual system can exist at several levels, connected by short vertical shafts. At Hunstanton, these levels are 5–6 cm. apart, running along the minor erosion surfaces within the *Paradoxica* bed, although elsewhere levels are up to 30 cm. apart (Text-fig. 4, A). The systems

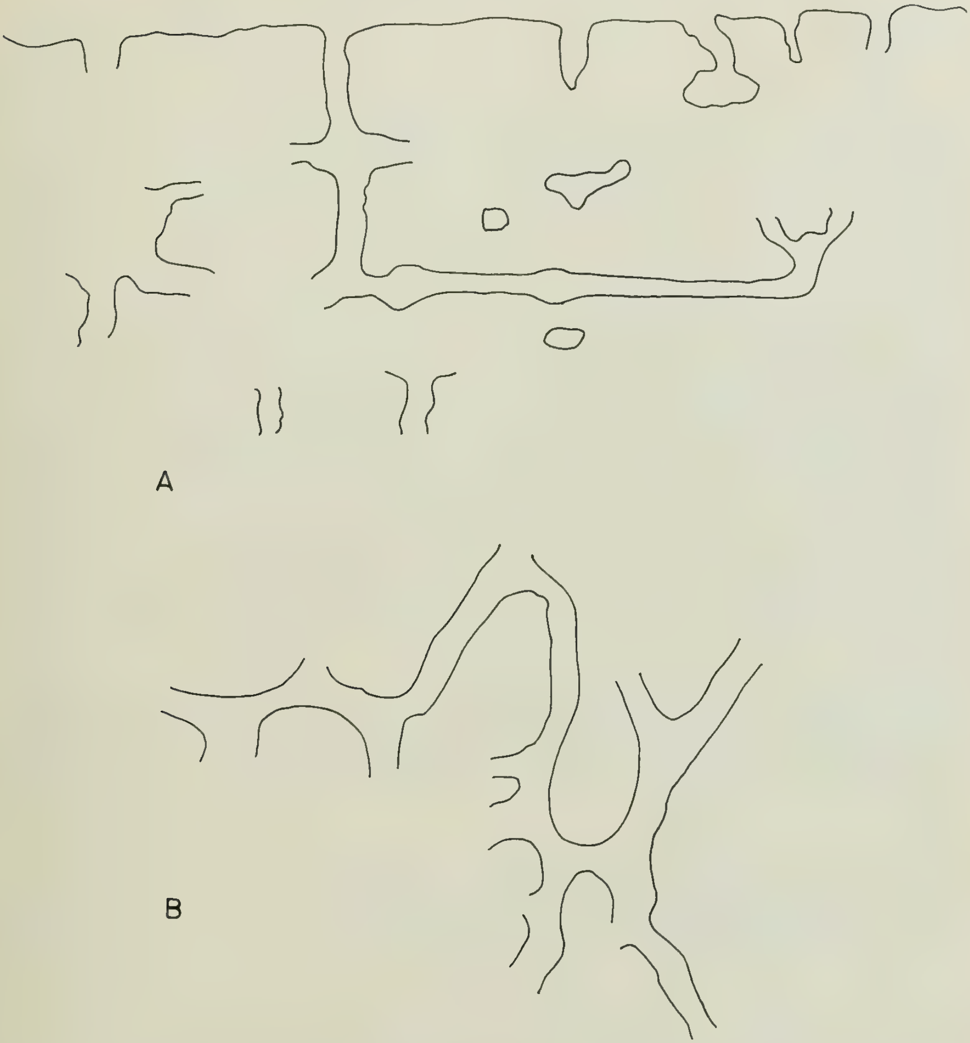


FIG. 4. *Thalassinoides paradoxica* (Woodward). A. Junction between Wilmington Sands and the overlying Middle Chalk; White Hart Sandpit, Wilmington, S. Devon. Vertical Section, $\times \frac{1}{8}$. B. Lower Chalk, Lower Cenomanian, Paradoxica bed; Hunstanton, Norfolk. Plan, $\times \frac{1}{8}$.

are connected to the surface by vertical or steeply inclined shafts 15–30 cm. long. On vertical faces, burrow densities are up to 20/1000 cm.^{2}

As pointed out by Hughes (1884) the surfaces of burrows have a green flakey coat; this appears to be glauconite. When cleaned, the surfaces of burrows are seen to be covered with rather poorly defined longitudinal ridges (Pl. 9, fig. 2).

Discussion. The name *Spongia paradoxica* was introduced by Woodward in 1830 in a " Synoptic table of British Organic remains ". In illustration, he referred to a figure in a paper by Webster (1814) " On some new variety of fossil Alcyonia ", recording it from Hunstanton and Southbourne. Subsequently (1833) Woodward recorded this form from the Red Chalk and Paradoxica bed. The figure referred to (Webster 1814, pl. 27, fig. 1) is in illustration of (p. 377) " an account of the singular organic body which I observed in the green sandstone stratum under the chalk " of the Isle of Wight. The figure is of a large block of Upper Greensand from the Undercliff along the southern coast of the island, present whereabouts of this specimen unknown ! Since Woodward records *Spongia paradoxica* from both the Red Chalk and Paradoxica bed at Hunstanton, other material, available for lectotype designation was clearly in Woodward's possession. His collection (or what remained of it) passed to the Norwich Castle Museum in 1836, and was incorporated in the collections. Much of the material, including figured specimens, was missing at the turn of the century, and although Mr. B. McWilliams of the Museum has searched the collections for any specimens of *S. paradoxica* from Woodward's collection, or labelled in his hand, none now remains which can be attributed to him. As a result, I have selected a specimen from the *Paradoxica* bed at Hunstanton as neotype.

Although first named by Woodward, these bodies were noted in 1823, in what must be one of the earliest records of a burrow from the chalk (albeit misidentified). Taylor (1823), describing the sequence in the cliffs at Hunstanton, Norfolk, noted as follows:

" *No. 4.* 1½ feet. A stratum of white chalk, more loose than the last, containing no fossil shells: yet it is to be distinguished by a remarkable ramifying zoophyte, resembling the roots of trees; about an inch thick, branching and intertwining in every direction. Some of the fragments are not unlike the horns of a stag."

This is the *Paradoxica* bed.

Again, later:

" *No. 6.* 2 feet. Red Chalk, of a rough disjointed structure, similar except in colour to No. 4, and like it, though in a smaller degree, interwoven with the ramifying zoophytes before mentioned."

The first use of the name *paradoxica* was by Woodward (1830: 5):

" *Spongia paradoxica.* Geol. Trans. ii. t.27, f.1. Red Chalk. Southbourn; Hunstanton."

The Southbourne occurrence would appear to be the same as that given by Mantell (1833), in a list of " Fossils from the chalk formation ", where a *spongia* from Southbourne (Sussex) is noted. In a footnote stating, " the inferior bed of marl which is in contact with the Firestone at Southbourne is almost entirely composed of zoophytes, milleporites, madreaporites etc., so as to form coral reefs "—presumably the Glauconitic Marl.

The specimens figured and described by Webster (1814) include a number of forms, both burrows and fossil sponges. Plates 27 and 29 represent burrows, plate 28, figures 3 (in part), 4, 8, 9, 10 and 11 represent the " tulip alcyonidium " (*Siphonia* *tulipa* Zittel). The nature of the specimens figured as pl. 28, figs. 5–7 is not clear, but they resemble *Cylindrites spongioides* (Goeppert 1842), here regarded as a crustacean burrow.

The next reference to " Spongia paradoxica " is by Woodward (1833 : 29): " Chalke Marle. This bed reposes upon the red chalk, and is seen to great advantage in that interesting section, Hunstanton cliff. It is of a grayish color, and at that place about four feet in thickness. The Spongia paradoxica, as we have named it *pro tempore,* abounds in it " . . .

Again, (p. 30):

" The Red Chalk . . . it is about two feet in thickness, and, like its superincumbent bed, abounds with Spongia paradoxica."

Rose (1835), describing the Red Chalk at Hunstanton speaks of " a ramose zoophite, the nature of which is not satisfactorily determined ". Again (p. 275), under the heading " Chalk without flints ", describes the lowest bed as being " made up of a ramose zoophyte, which strongly characterizes it ", regarding it (p. 276) as " best explained by supposing it originally a coral reef and its interstices filled with Cretaceous Mud."

Wiltshire (1859: 275), in a list of fossils from the Red Chalk records " Spongia paradoxica Geol. Trans. 2, tab. 27, fig. 1. page 377 (In the collections of Mr. Rose and Author.) ". Later (p. 277, footnote): " Siphonia pyriformis is probably the head of Spongia paradoxica. In the cabinet of Mr. Rose is a mass of the latter, to which a head similar to the one figured is attached ". The figures referred to are the first of *S. paradoxica* from Hunstanton published. Wiltshire's pl. 1, fig. 1, shows a typical branching fragment, fig. 2, referred to as *Siphonia pyriformis* is a swollen cylindrical body, the terminal portion being flat, with a circular depression surrounded by a raised rim.

Seeley (1864), refers to " organic growth known as ' spongia paradoxica ' in the sponge bed and top of the red chalk ". Wiltshire (1869), describing the Hunstanton section, notes " a meandering and many-branched sponge, *Siphonia paradoxica* " from his bed b (the Paradoxica bed), whilst " *Spongia paradoxica* Webster ", is recorded from the highest band of the Red Chalk.

By far the most extensive discussion is that of Hughes (1884) who concludes (257–277) that Webster's figure is a different fossil, the " tulip alcyonidium ", and that the fossil *Spongia paradoxica* is in fact an inorganic body, as sponge structure is preserved in the surrounding rock, but never in *S. paradoxica*. Large shell fragments in the matrix indicate conditions unsuitable for a delicate sponge, fragments of the *Spongia* are never found in the matrix, whilst shell fragments are avoided and never encrusted as would be expected in the case of a sponge.

This inorganic origin is accepted by Whitaker & Jukes-Browne (1899) who repeat Hughes' views, and Jukes-Browne (1900, 1903), who refers to " curious cylindrical bodies . . . which resemble the stems of *Siphonia* but which do not contain any sponge structure ". The most recent account of this " organism " is that of Peake & Hancock (1961), describing the *Paradoxica* bed:

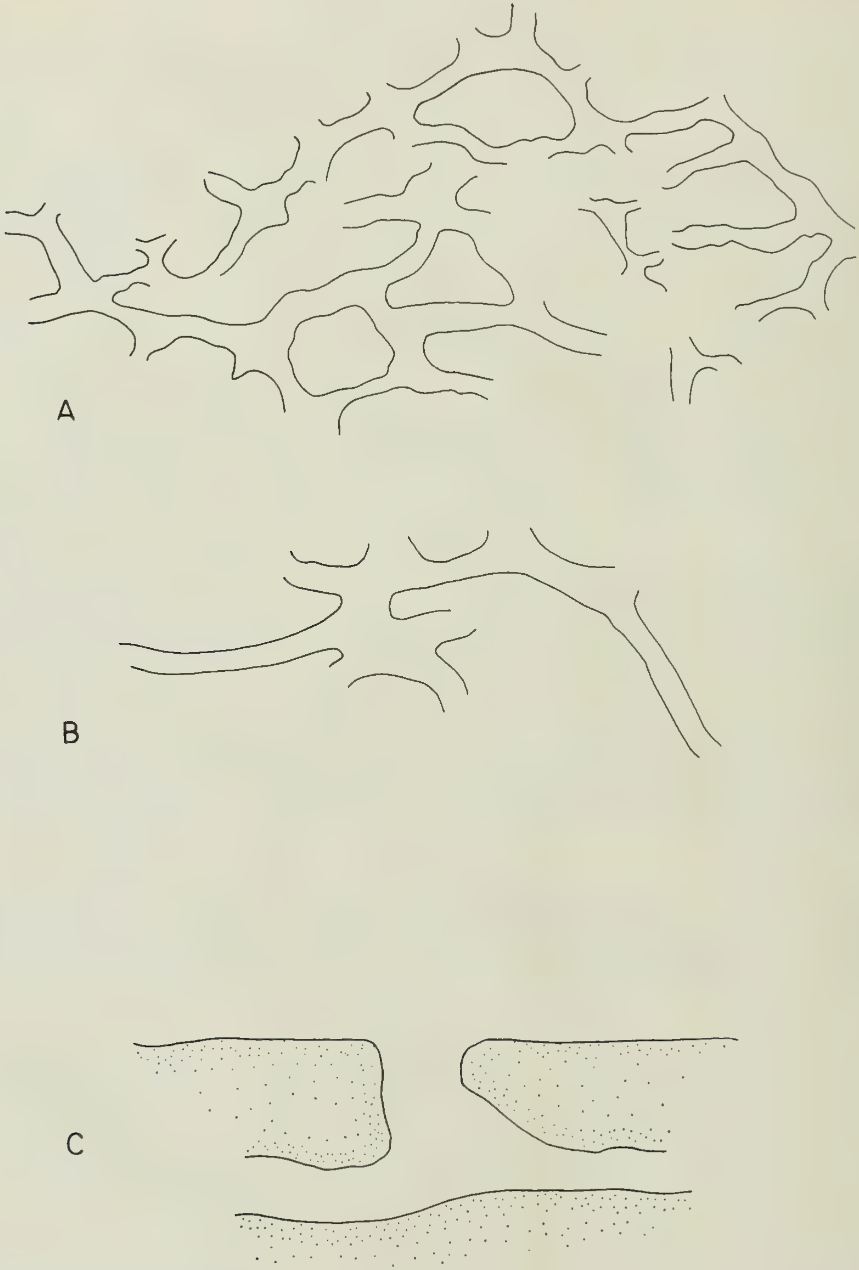


FIG. 5. A, B. *Thalassinoides paradoxica* (Woodward). A, Lower Chalk, Lower Cenomanian, Paradoxica bed; Hunstanton, Norfolk. Plan, $\times \frac{1}{8}$. B, Middle Chalk, Lower Turonian, Melbourn Rock; Brockham Limeworks, Betchworth, Surrey. Plan, $\times \frac{1}{4}$. C. *Thalassinoides* sp. Lower Chalk, Middle Cenomanian; cliffs below Whitbred Hole, Eastbourne, Sussex. Vertical section showing entrance shaft, $\times \frac{1}{2}$.

" soft-bodied organisms have left casts of their burrows which now form radiating, cylindrical branching and intertwining masses; they were once thought to be sponges, and actually named *Spongia paradoxica* ".

Häntzschel (1962) includes "*Spongia paradoxica* Woodward 1833 (=*Siphonia paradoxica* AUCTT.) " in a list of unrecognized and unrecognizable genera of trace fossils, giving Taylor's description and Hughes' views on its inorganic origin.

I have no doubt that this is a *Thalassinoides*, from both mode of branching and scratches; and that it is a crustacean burrow. The irregular three-dimensional branching makes it readily separable from other forms of *Thalassinoides*. The short blind burrows give a superficial resemblance of some parts to *Spongeliomorpha*.

Apart from its record in the English literature, already discussed, this type of burrow was described as early as 1760 by Schulze, who regarded them as crinoid remains. Problematic structures figured by Geinitz (1871) from the German Upper Cretaceous are clearly *T. paradoxica*. *Spongia sudolica* Zareczny (1878), regarded by Raciborski (1890) as a *Spongeliomorpha*, resembles *T. paradoxica* in size, but has rather different ornament; it is clearly a *Thalassinoides*.

In Britain, *T. paradoxica* has a very limited distribution, occurring only in association with minor erosion surfaces and signs of early lithification-hardgrounds. At Hunstanton the burrows occur associated with the erosion surfaces at the top of the *Paradoxica* bed, the Red Chalk and a minor erosion surface within the *Inoceramus* bed. The burrows in the *Paradoxica* bed tend to spread out along the minor erosion surfaces within the bed, but often pass through them. At the base, they follow the undulating irregular surface of the Red Chalk, but never pass into it. Those in the overlying *Inoceramus* bed follow the surface of the *Paradoxica* bed in like fashion. In both cases, the burrows always avoid pebbles, large shell fragments and echinoid tests, indicating that the animals could not bore into hard objects. That the erosion surfaces at the top of the Red Chalk and *Paradoxica* bed are never penetrated, likewise indicates that these were lithified when the burrowers were active in the sediment above. In the burrows beneath the Chalk Rock, here preserved as empty cavities, brachiopods, echinoids and *Inoceramus* fragments protrude into *Thalassinoides* burrows, the surrounding sediment having been removed, whilst the hard shell was left, again indicating inability to deal with hard objects.

In the south, the top of bed B. in the Wilmington outlier is penetrated by *T. paradoxica* (Text-fig. 4, A), here to a much greater depth, as there is no lower hardground to limit penetration. The burrows are excavated in sandstone, and are full of glauconitic chalk with small phosphates, identical with that in the base of the overlying Middle Chalk (equivalent to bed C. of the coastal sections). The walls of these burrows have a phosphatic veneer, as does the overlying erosion surface, whilst the sediment immediately around the burrows is impregnated with glauconite; this suggests that the lithification prior to these processes occurred either whilst the burrows were still occupied, or in the period before they were filled by drifted material.

This same trace-fossil occurs, associated with hardgrounds, at the top of beds A_2 and B of the Cenomanian Limestone on the Devon coast. It is also present, associated with hardgrounds, in the Middle Chalk above, and elsewhere in Southern England in the Melbourn Rock, again associated with hardgrounds. In the Lower

Chalk, it occurs below a hardground 11 m. below the *plenus* Marls at Culver Cliff (Isle of Wight).

In every case there is evidence that the burrow was excavated in soft sediment, and that the hardening, phosphatization and glauconitization, some or all of which occur in the associated hardground, post-date burrowing, but seem to have occurred prior to their silting up.

I have never seen any comparable burrow systems in chalk away from hardgrounds, and believe the association to be a valid one.

The " tubulures " of many continental authors, occurring associated with hardgrounds, variously interpreted as tree-roots, algae, annelid, terebellid or crustacean burrows (Schroeder & Böhm 1909, Ellenberger 1946, 1947, Marlière 1933 etc.), are clearly burrows of a similar type.

Occurrence. The distribution and occurrence of *T. paradoxica* is fully dealt with in the discussion above.

Ichnogenus ***CHONDRITES*** Sternberg 1833

Diagnosis. " Very plant-like, regularly ramifying tunnel structures which neither cross each other nor anastomose; should be interpreted as dwelling burrows or feeding burrows; width of tunnels remaining equal within a system, otherwise varying from large (i.e. *Buthrotrephis*) to small (e.g. *Chondrites*) very common trace fossil, usually named fucoid . . . surface pattern commonly very regular, effected by phobatactis . . . (probably made by marine worms). Cambrian to Tertiary. Cosmopolitan " (Häntzschel 1962 : 187–188).

Type species. *Fucoides targionii* Brongniart, by the subsequent designation of Andrews (1955).

Discussion. The synonymy of *Chondrites* is given by Häntzschel (1962). Scott Simpson (1957) has discussed this trace fossil at length, reviewing early interpretations and concluding that it is the feeding-trace of some worm-like organism.

The following features have been indicated as diagnostic (Simpson 1957):

(a) Circular cross-section.
(b) Constant diameter (in some cases with constrictions at the point of branching).
(c) Smooth wall.
(d) Regular branching pattern:
    (i) Branching tends to be pinnate, especially at the periphery of the system, when not interfered with by neighbouring systems.
    (ii) Branching is always lateral, never equal.
    (iii) A large number of orders of branching may be present.
    (iv) The pattern lacks symmetry other than a radial tendency.
(e) Attitude, with both vertical and horizontal elements, the latter undergoing extensive ramification.
(f) Phobotactic pattern.

Chondrites sp.

(Pl. 2, figs. 2, 4; Pl. 5, fig. 3; Pl. 9, fig. 1)

A small species of *Chondrites* with tunnel diameters between 1 and 2 mm. is common throughout the whole of the Lower Chalk.

Many of the small, horizontal or gently inclined burrows present can be referred to this genus; every section I have examined contains this form, which is also occasionally encountered in the Glauconitic Marl.

Horizontal sections show that the vertical elements of these systems have a circular cross section; vertical sections show that the horizontal or gently inclined elements have an elliptical section, presumably as a result of compaction (which can be demonstrated by the crushing and deformation of associated fossils). Diameters are very constant, varying between 1 and 2 mm. in specimens from many horizons and localities. Individual branches and systems show a constant diameter throughout. Tunnel walls are smooth, tunnel fills structureless. Tunnels are always straight, except at the point of branching.

Vertical elements are less abundant than horizontal or inclined parts. No example of the two joining up has been observed but a sharp change of direction is implied. Sections give only limited information about branching but show this to have been lateral, never equal and at an acute angle. Horizontal and inclined elements branch frequently, vertical elements rarely.

Burrows never intersect, suggesting a phobotactic behaviour pattern: more positive evidence is seen in sections which suggest a " wrapping around " of tunnels, embracing on close encounter, then continuing in the original direction. " Solid " specimens—chance fracture surfaces (Pl. 9, fig. 1) or the cleaned surfaces of larger burrows from beneath the Totternhoe Stone (Pl. 5, fig. 3) give a better picture of the mode of branching. All the features already noted are present. There is no obvious symmetry; first and second order branches are present, branching at acute angles; pinnate branching is occasionally seen. Phobotactis is expressed in terms of " embracing " and stopping short. From these features, reference to *Chondrites* is clearly justified.

There are a wide variety of names available for forms of this size and it seems pointless to name the present material.

As noted above, every section contains these burrows: the maximum observed density is about 20 sections per square centimetre. A very characteristic occurrence of *Chondrites* is in the filling of larger burrows (Pl. 2, fig. 4). In nearly every instance, *Chondrites* is far more abundant in these than in the surrounding sediment; *Thalassinoides* is particularly prone to this re-working. Beneath the Totternhoe Stone at Houghton Regis, the filling of *T. saxonicus* burrows is completely re-worked and the bottom surface of the burrow converted to a felted mass of *Chondrites* (Pl. 5, fig. 3), whereas this form is uncommon at the base of the Totternhoe Stone and penetrates only a few centimetres. *Chondrites* penetrates to a much greater depth in burrow fillings than the surrounding sediment; a similar feature has been noted by Seilacher (1964 : 302, text-fig. 3, right-hand figure), *Chondrites* penetrating to a greater depth in the septum of a *Corophioides* than in the surrounding sediment (Lias γ, S. Germany).

A number of alternative explanations can be offered:

(i) The filling of the larger burrows is richer in nutrients than the surrounding sediment.
(ii) Re-worked sediment is better oxygenated.
(iii) Re-worked sediment is softer and thus more readily penetrated.

Of these alternatives, I would favour (iii) in view of the occurrences beneath the Totternhoe Stone where the presence of other burrowers, feeding on sediment, suggests it contained nutrients and was suitable for burrowing.

The abundance of *Chondrites* on the lower surface of larger burrows suggests that there is a geotropic control on the direction of burrowing, and that the sediment surrounding the burrows is not penetrated suggests that it was too stiff for the *Chondrites* animal. The surfaces of *Gyrolithes,* as figured by Saporta (1884) are covered by *Chondrites* in a similar fashion. An alternative may be that the *Chondrites* animal was feeding on mucus lining the burrow.

Ferguson (1965) has suggested that the filling of *Chondrites* tunnels was by the sucking-in of sediment from the surface-opening of the system as soon as the proboscis (or whatever part of the animal produced the burrow) was withdrawn from a branch. The arguments for this mode of filling are very reasonable, but it should be noted that ammonite siphuncles, borings and echinoid stereomes are sometimes sediment filled, indicating that passive filling of such structures can occur.

OCCURRENCE. *Chondrites* sp. occurs in all sections of Lower Chalk examined. Comparable forms occur occasionally in the Glauconitic Marl and are common in the *plenus* Marls.

Ichnogenus ***SPONGELIOMORPHA*** Saporta 1887

1887 *Spongeliomorpha* Saporta : 299, pl. 6, figs. 2, 3.
?1913 *Rhizocorallium*; Felix : 21 (non Zenker).
1945 *Spongiliomorpha*; Darder, plate 8 (errore).
1955 *Spongeliomorpha*; de Laubenfels : E 36.
?1955 *Felixium*; de Laubenfels : E 36.
1962 *Spongeliomorpha*; Häntzschel : W 216.
?1965 *Felixium*; Häntzschel : 35.
1965 *Spongeliomorpha*; Häntzschel : 87.
1965 *Spongiliomorpha*; Häntzschel : 87.

DIAGNOSIS. Medium sized, elongate, cylindrical, branching tunnel system, surfaces covered with network of fine ridges, interpreted as scratch marks; probably produced by crustaceans. Range: Triassic to Miocene.

TYPE SPECIES. *Spongeliomorpha iberica* Saporta 1887 (299, pl. 6, figs. 2, 3) from the Miocene of Alcoy, Spain, by monotypy.

DISCUSSION. Saporta (1887) described what he believed to be a new form of keratosid sponge, *Spongeliomorpha iberica,* based on material from the Miocene of Alcoy (Spain), comparing it with *Spongelia* Nardo (in fact a synonym of *Dysidea*

Johnson: see de Laubenfels 1955: E 536), a form ranging from Eocene to Recent. In addition to the type material, Saporta mentions other material from the Calcaire Grossier and the United States. The fossil is indicated as resembling the horns of a deer, and being associated with *Taonurus* Saporta (=*Rhizocorallium* Zenker), a " fucoid ". Meunier (1889) described, without figuring, the material noted from the Calcaire Grossier. This new form, *Spongeliomorpha saportai* Meunier, from the " Sables du Beauchamp ", above the Calcaire Grossier, differs from *S. iberica* in its more elongate form and tendency to dichotomous branching (the specimen is 22 cm. long with a diameter of 2 cm.; lateral second and third order branches are present). The surface is said to be covered by ridges more regular, parallel and uniform than in *S. iberica*. Interpretation of *Spongeliomorpha* as a sponge is supported by Reis (1910), who describes Triassic forms, and de Laubenfels (1955) who compares it to the Jurrassic form *Spongelites* Rothpletz, a genuine sponge. Darder (1945) figures " *Spongiliomorpha* " *iberica*, again from the Miocene (Burdigalian) of Alcoy, but regards it as algal, and a sexual dimorph of *Taonurus ultimus* (i.e. a *Rhizocorallium*) ! The most satisfactory explanation is that of Reis (1922) who interpreted *Spongeliomorpha* as a burrow system.

The genus *Felixium* de Laubenfels (1966), proposed to replace *Rhizocorallium* Felix (1913, non Zenker) with *R. glaseli* Felix (*gläseli* recte = *glaeseli*) as type species, appears to be a burrow, perhaps a *Spongeliomorpha*, perhaps a *Thalassinoides* fragment or even the " arm " of a *Rhizocorallium*.

Scratched burrows for which the name *Spongeliomorpha* seems suitable have been discussed and figured by Lessertisseur (1955) from the marine Hauterivian of Andon (Alpes-Maritimes, France) and Weigelt (1929) from the Jurassic and Cretaceous of Germany. Raciborski (1890) regarded *Spongia sudolica* Zareczny (1878) as a *Spongeliomorpha*; from the branching pattern it is clearly a *Thalassinoides*, possibly a synonym of *T. paradoxica* (vide p. 147).

The figured material of *Spongeliomorpha* is all in the form of small fragments. The original figured specimen agrees closely with some fragments of *Thalassinoides paradoxica* in general form, whilst the ornament of *Spongeliomorpha* and *Thalassinoides ornatus* suggests that when the branching form of *Spongeliomorpha* is better known the two names may prove synonymous. *Spongeliomorpha* is used in the present account for scratched burrows which do not show a *Thalassinoides*-like branching.

The surface ridges of *Spongeliomorpha* are regarded as having the same origin as those of *Thalassinoides*—as a result of the inhabitant digging or moving through the system. Once more, only two groups of animals seem likely to produce these markings, crustaceans and annelids. Since Weigelt (1929) has figured similar scratches on Recent crustacean burrows whilst the same ornamentation is present on the fossil crustacean burrow *Rhizocorallium* (Weigelt 1929, Abel 1935, Häntzschel 1962), a crustacean origin for *Spongeliomorpha* is clear. Similar ornamentation is also seen on the undoubted crustacean burrow *Ophiomorpha* (personal observation based on material from the English Weald Clay (Lower Cretaceous, Barremian)).

Spongeliomorpha sp.

(Pl. 7, fig. 7)

Fragments of a *Spongeliomorpha* are not uncommon in the Lower Chalk at every locality examined. By far the best locality is beneath the Totternhoe Stone at Houghton Regis. The cross section is elliptical (presumably as a result of compaction), varying between 30 by 18 mm. to 16 by 12 mm. Straight or slightly curved fragments are commonest and occur in both vertical and horizontal positions. Occasional narrow lateral branches may be present. The surface is covered by small, sharp reticulate ridges intersecting at 80 and 100 degrees. No internal structure; surface often covered with small *Chondrites* and other burrows.

In size and general form these fragments are closely comparable to *S. iberica*, differing in their less continuous ridges intersecting at a higher angle. None of the material I have seen shows the antler-like branching of the figured specimens.

OCCURRENCE. Frequent in all sections of the Lower Chalk examined.

Spongeliomorpha? annulatum ichnosp. nov.

(Pl. 2, fig. 1; Pl. 5, fig. 5; Text-fig. 6, E)

DIAGNOSIS. Cylindrical branching burrows consisting of a marl cylinder 1–2·5 cm. in diameter with a glauconitic core 5 mm. in diameter; outer surface covered by longitudinal ridges. Occurring in glauconitic sediments.

HOLOTYPE. B.M. (N.H.) T.554 from the Glauconitic Marl (Lower Cenomanian); section below the Martello Tower No. 3, Folkestone, Kent.

MATERIAL. In addition to the holotype, I have examined many hundreds of specimens from the Glauconitic Marl and Upper Greensand of Southern England.

LOCALITY AND HORIZON. Abundant in the Glauconitic Marl at all localities examined. Occurring also in glauconitic bands above the base of the Chalk and in the glauconitic basement bed of the Lower Chalk in the south-west. Very common at many localities and horizons in the Upper Greensand. Widespread in glauconitic facies of Cretaceous age all over north-west Europe (J. M. Hancock, personal communication).

DESCRIPTION. Largely horizontal, cylindrical in section with diameters between 1·0 and 2·5 cm. Branching poorly known, apparently alternate and at an acute angle (fig. 6, E). Occurring only in glauconitic sediments, the burrow consists of a glauconite-free marl cylinder with a central glauconitic core about 5 mm. in diameter. The outer surface of the marl cylinder is covered in longitudinal ridges.

DISCUSSION. For over 150 years geologists in this country have noted the presence of " stem-like " markings in the Glauconitic Marl and other glauconitic Albian and Cenomanian sediments. Webster (1814) regarded these structures as alcyonites (sponges). Reid (1898), describing the Upper Greensand near Beachy Head, Eastbourne (Sussex) mentions . . .

" curious cylindrical cavities filled with material differing somewhat from the surrounding matrix. These are perhaps made by some boring animal, though the horizontal position and closed ends often suggest rather the disappearance of buried sand-eating Holothurians."

They are perhaps the " irregular spots and veinings of white marl " noted by Jukes-Browne & Hill (1903 : 38) from the Glauconitic Marl at Folkestone (Kent), later (p. 265) described as being . . . " areas of small size—seen in the hand specimen as whitish markings or pipings are filled with fine amorphous calcareous material to the exclusion of the larger glauconite grains ". What are probably the same burrows are noted by Thomel (1961) from an Upper Albian greensand from the Alpes–Maritimes, France.

Although extremely abundant in most sections of Glauconitic Marl and Upper Greensand (tunnel densities up to 80 per 1,000 cm.^{2}), the branching pattern is poorly known. The surface ornamentation of ridges suggests reference to *Spongeliomorpha*, but because of the peculiar internal structure a new generic name may be useful for this type of burrow.

Interpretation. For reasons already stated, the surface ridges of these burrows are interpreted as scratch marks produced by crustaceans. The peculiar internal structure can be interpreted as a result of the sifting of sediment into clay, silt and sand grade materials during feeding, the animal presumably living on small organisms in the coarse fraction.

Ichnogenus ***PSEUDOBILOBITES*** Lessertisseur 1955

1882 Pseudobilobites, Barrois : 175, pl. 5, fig. 5*a*, *b* (not intended as a generic name).
1955 Pseudobilobite, Lessertisseur, text-fig. 25, G.
1955 *Pseudobilobites* Barrois; Lessertisseur : 45.
1965 ,, Pseudobilobites " Barrois; Häntzschel : 75.

Diagnosis. Medium sized (3–7 cm. long) rounded or oval masses of sand-grade microfossils (largely foraminifera) and shell fragments cemented by calcite, generally ironstained, due to oxidation of small quantities of pyrite present. Upper surface flat or concave, smooth or slightly granulated. Lower surface convex, convoluted, covered by groups of short parallel ridges inclined at an angle to the axis of the structure.

Type species. *Pseudobilobites jefferiesi* ichnosp. nov., here designated. Lower Chalk, Middle Cenomanian; Pitstone (Bucks).

Discussion. The term " pseudobilobite " was first used by Barrois (1882), in a discussion of *Bilobites* (=*Cruziana*)—resting trails of trilobites, from the Palaeozoic of Northern Spain. Clearly intended as a vernacular name, he applied it to small oval masses of microfossils, the lower surfaces of which are covered in ridges, from the Lower Turonian of Séry in the Ardennes.

Lessertisseur (1955) uses the term rather ambiguously: in the explanation of his figure 25 G (a copy of Barrois 1882, pl. 5, fig. 5*a*) he uses the name in the vernacular, on page 45, the name is italicized, as are the other generic names in Lessertisseur, and Barrois is given as author, together with the reference. Clearly, it is regarded as of generic status. As already noted, Barrois regarded Pseudobilobites as a vernacular name; Lessertisseur's use as a generic name, with Barrois as author is not justified. The genus *Pseudobilobites* is, therefore, attributed to Lessertisseur 1955.

The " problematicum " of Jefferies (1962, 1963) is clearly a trace fossil of this type. Similar forms occur in the Lower Chalk and are described as *Pseudobilobites jefferiesi* ichnosp. nov., here designated type species of *Pseudobilobites*.

Pseudobilobites jefferiesi ichnosp. nov.

(Pl. 6, fig. 1; Pl. 7, fig 3; Pl. 8, fig. 4; Pl. 9, figs. 3, 4, 6)

1961 *Problematicum* sp., Jefferies, text-fig. 2.
1961 Problematicum, Jefferies : 620, 623, 624, 644, pl. 77, fig. 5.
1963 Problematicum sp., Jefferies : 7, 12, 14, 16, 17, text-fig. 2 (pars.).

DIAGNOSIS. As for Genus.

HOLOTYPE. B.M. (N.H.) T.565. Lower Chalk, Middle Cenomanian; Pitstone (Bucks.).

MATERIAL. Paratypes, B.M. (N.H.) T.556, 566, Lower Chalk, Upper Cenomanian, 10–15 ft. below base of *plenus* Marls; below Shakespeare Cliff, Dover, Kent. Numerous other specimens from the Lower Chalk and *plenus* Marls (Sedgwick Museum, Cambridge, Jefferies collection).

DESCRIPTION. Small ovoid masses of sand-grade microfossils (foraminifera) and shell fragments, cemented by crystalline calcite and stained brown by limonite, derived from the decomposition of the small quantities of pyrite present in unweathered specimens. In shape, specimens vary from elongate ovals, half as wide as long, to almost circular, ranging in length between 3 and 7 cm., although larger specimens probably also occur. The outline is fairly regular, although often broken up by subsequent burrowing. Upper surface smooth or slightly granular, flat or slightly concave, lower surface convex, convoluted and irregular, covered by groups of short, parallel ridges, inclined to the long axis of the structure.

DISCUSSION. The original specimen figured by Barrois (1882) differs from *P. jefferiesi* in having longer more continuous ridges on the (presumed) under-surface. The figure is rather indifferent and re-examination of the material may indicate that it is the same as the present form.

These structures were first recorded from the English Chalk by Jefferies (1962, 1963) who briefly described and illustrated a " problematicum " from the top of the Lower Chalk and the *plenus* Marls. Subsequent collecting shows that they are common throughout the whole of the Lower Chalk, and also occur in the Melbourn Rock at the base of the Middle Chalk. Specimens show great shape variation in both outline, thickness and convexity, but form a quite distinctive group of trace fossils.

In thin section, the constituents are clearly the coarse fraction of the chalk. Foraminifera are abundant, ostracods, shell and echinoid debris plus small masses of collophane (? faecal pellets) make up the remainder, with a calcitic cement. Burrows passing through these structures suggest they were soft when buried, and that they are not of diagenetic origin (Pl. 9, fig. 6). Occasionally, internal laminations are present. *Pseudobilobites* clearly represents a type of activity like that which produced what I have called " laminated structures ". The prominent ridges on the base I would interpret here, as elsewhere, as scratch marks, indicative of crustaceans. Grouping in threes, fours or fives represents either the co-ordinated movement of appendages, or movement of a single appendage with several claws. From an examination of these structures in situ, they appear to be a surface trace. I have never seen a convincing example in a burrow, although the possibility cannot be overlooked.

This type of structure could result from the feeding activities of an animal sifting chalk for the fine fraction, ingesting this and leaving the coarse debris behind. The lower, scratched surface, represents the extent of foraging, the concave upper surface is perhaps an expression of the position of the body during feeding.

Not all the segregations of coarse debris in the Lower Chalk belong to this form, some (including, in part, some of the " problematicum " recorded by Jefferies (1961, 1963)) represent the partial or total filling of vertical and horizontal cylindrical burrows (a typical fragment is represented in Pl. 6, fig. 2). This type of filling probably represents the same type of activity. They sometimes occur closely associated with " laminated structures " (Pl. 8, fig. 3) and may be the product of the same animal, although separate occurrences show that these could be chance associations.

P. jefferiesi is widespread and common in the Lower Chalk and *plenus* Marls, also occurring in the Melbourn Rock (Lower Turonian).

***Keckia*(?) sp.**

1911 *Keckia* (?) sp., Bather : 553, pl. 24, fig. 1.

Bather's account of this form is excellent, as is his illustration. Having seen no other material, I can add nothing to his account. The nature and interpretation of *Keckia* has been discussed by Häntzschel (1938) and by Richter (1947).

" *Terebella* " *cancellata* Bather

(Pl. 8, figs. 1, 2)

1897 *Terebella lewesiensis* (Mantell) Davies; 145–148 (pars.).
1911 " *Terebella* " *cancellata* Bather : 551–553, 556, pl. 24, figs. 3, 4, No. 5.

DIAGNOSIS. " Tube from which the (?gelatinous or mucilaginous) wall has disappeared, leaving on the internal cast an obscure cancellate ornament formed by transverse and longitudinal folds; with diameters from about 0·75 to 2 cm. and with a possible length of 19 cm. or more " (Bather 1911).

HOLOTYPE. B.M. (N.H.) 58253, Lower Chalk, Glynde, Sussex, figured here as Plate 8, fig. 1.

DISCUSSION. Bather's description of this " Terebellid " is excellent, but I believe his interpretation to be erroneous. "*Terebella*" *cancellata* is clearly a burrow; material agreeing with the holotype and the holotype itself all appears to represent poorly preserved burrows of a type agreeing with what I have called *Spongeliomorpha* sp. The surface depressions described by Bather (1911) are the result of rather poorly preserved intersecting ridges (i.e. scratches). The paratype specimen, B.M. (N.H.) 1574 (Pl. 8, fig. 2) clearly belongs to a different form and is described below, as burrow type D.

From a re-examination of the holotype of "*Terebella*" *harefieldensis* White (White 1923), here figured for the first time, as Plate 7, fig. 2, it is clearly identical with crustacean " burrows " figured by Weigelt (1929), from a similar occurrence in Germany. *T. harefieldensis* is not a true burrow; excavated in hard chalk, below the sub-Tertiary erosion surface it is to be regarded as a boring. From its widespread distribution (Hester 1965, text-fig. 2) recognition as a crustacean boring may give this form value as a palaeogeographic indicator. No generic name appears to be available for this type of boring.

V. OTHER BURROWS

The forms described above constitute only a part of the trace fossil assemblage of the Lower Chalk. Some of the more obvious burrows, too poor for detailed study are noted below.

BURROW TYPE A

(Text-fig. 6, B, C)

DESCRIPTION. Burrow system made up of four vertical cylindrical shafts between 6 and 12 cm. long, widening downwards, connected by a horizontal tunnel 16–30 cm. long. Tunnel diameters about 2 cm.

DISCUSSION. I have seen only two complete systems of this type. The systems originate at the bases of marls, piping down into the limestones below. The nature of the openings is not clear, but the vertical shafts increase in diameter away from the surface and are at their widest just above the junction with the horizontal tunnel. The spacing of shafts is identical in both examples I have seen: one shaft lies at each end, the other two are equidistant from each other, but one is separated from the end by nearly twice the distance separating the two inner shafts.

I have seen no descriptions or figures agreeing with these systems, and in view of the identical form of the two examples, I am inclined to regard this as a new form.

The most similar described system is that of *Pholeus abomasiformis* Fiege (Fiege 1944, Häntzschel 1962, 1965) from the Trias (Muschelkalk) of North Germany. *Pholeus* differs from the present form in the absence of intermediate shafts and the presence of a swollen horizontal chamber. *Pholeus* is regarded as a decapod crustacean burrow. The burrow of the living crustacean *Cambarus carolinus* Erichsen (Fiege 1944, fig. 3) is again similar but a swollen portion (" living chamber ") is present.

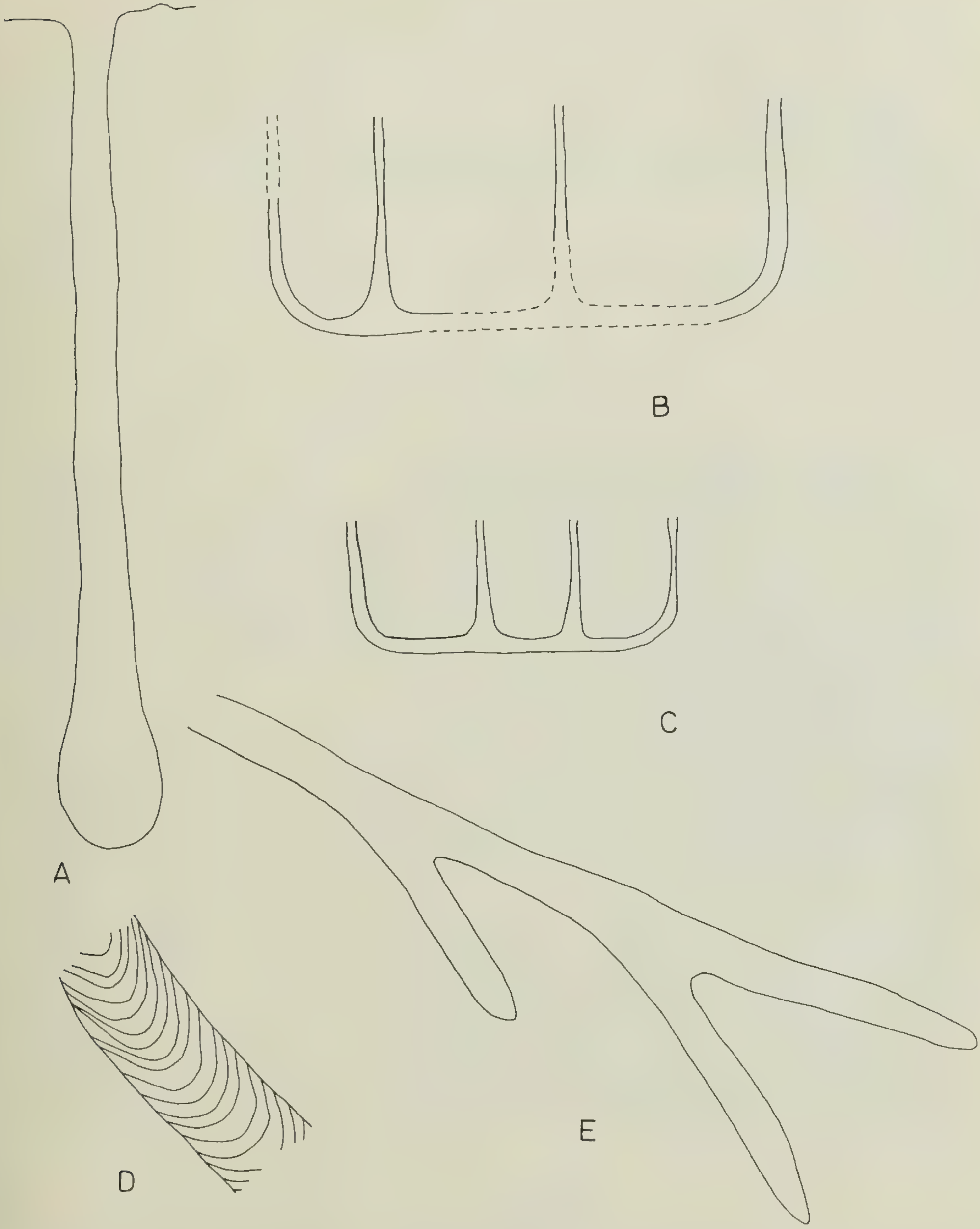


Fig. 6. A, Burrow type B, Top of Wilmington Sands, filled by the overlying Middle Chalk; White Hart Sandpit, Wilmington, S. Devon. Vertical section, × $\frac{1}{8}$. B, C, Burrow type A, Lower Chalk, Middle Cenomanian. B, Folkestone, Kent, C, Eastbourne, Sussex. Both vertical sections, × $\frac{1}{4}$. D, *Thalassinoides* sp. Lower Chalk, Middle Cenomanian; Hunstanton, Norfolk. Plan, showing septate internal filling. × 1. E, *Spongeliomorpha? annulatum* ichnosp. nov. Upper Greensand; Cow Gap, Eastbourne, Sussex. Plan, × $\frac{1}{2}$.

There is a superficial similarity to the tube system of the living polychaete *Lanice* (Seilacher 1951, Schaefer 1962) but the Chalk form lacks a lining.

This system cannot be compared with the simple U-shaped burrow of worms such as *Urechis* (MacGinitie 1928) or fossil representatives such as *Arenicolites*, as the presence of four openings would render the functional purpose of the burrow, in terms of maintenance of respiratory and feeding currents, too complex.

There is insufficient evidence to suggest the nature of the inhabitants of this type of system.

Occurrence. The two perfect specimens are from the Middle Cenomanian of Folkestone and Eastbourne.

Burrow Type B

(Text-fig. 6a)

Description. Vertical, cylindrical burrows up to 5 cm. in diameter and 100 cm. long. Bottom swollen into an elongate chamber.

Discussion. Large simple burrows of this type are not uncommon in the upper part of the sandy facies of the Cenomanian at the White Hart Sandpit, Wilmington, S. Devon. The burrows are in the equivalent of bed B. of the coastal sections, arising from the erosion surface at the top of this division and filled with the overlying sandy glauconitic Middle Chalk. The walls of these burrows, like the associated *T. paradoxica* have a phosphatic veneer and the sediment immediately surrounding the burrows is impregnated with glauconite.

Similar burrows have been described and figured by Lessertisseur (1955) from the Eocene (Bartonian) of the Paris Basin and by Maubeuge & Lanly (1952) from the Bathonian of the Vosges. A similar but much smaller form occurs in the Folkestone Beds (Lower Albian) away from the coastal type section, as at Aylesford (Kent), and in the Woolwich Bottom Bed (Eocene) at Upnor, (Kent). Some of the specimens of *Cylindrites spongioides* figured by Goeppert (1842, pl. 46, figs. 1–4) may be burrows of this type.

These burrows are very similar to those of intertidal crustaceans from the East Indies described by Verwey (1930), and are here interpreted as the work of crustaceans, although it is not implied that these were intertidal.

Occurrence. Top of Wilmington Sands (bed B), filled with Middle Chalk; White Hart Sandpit, Wilmington, S. Devon. Similar burrows occur in the bioclastic Santonian of the Sudmerberg near Goslar on the north flank of the Hartz (J. M. Hancock, personal communication).

Burrow Type C

(Text-fig. 7)

Description. Long, straight or slightly flexed, very narrow cylindrical burrows up to 40 cm. long and between 1 and 10 mm. in diameter. Both vertical and horizontal elements occur, the latter often much narrower than the vertical part, from

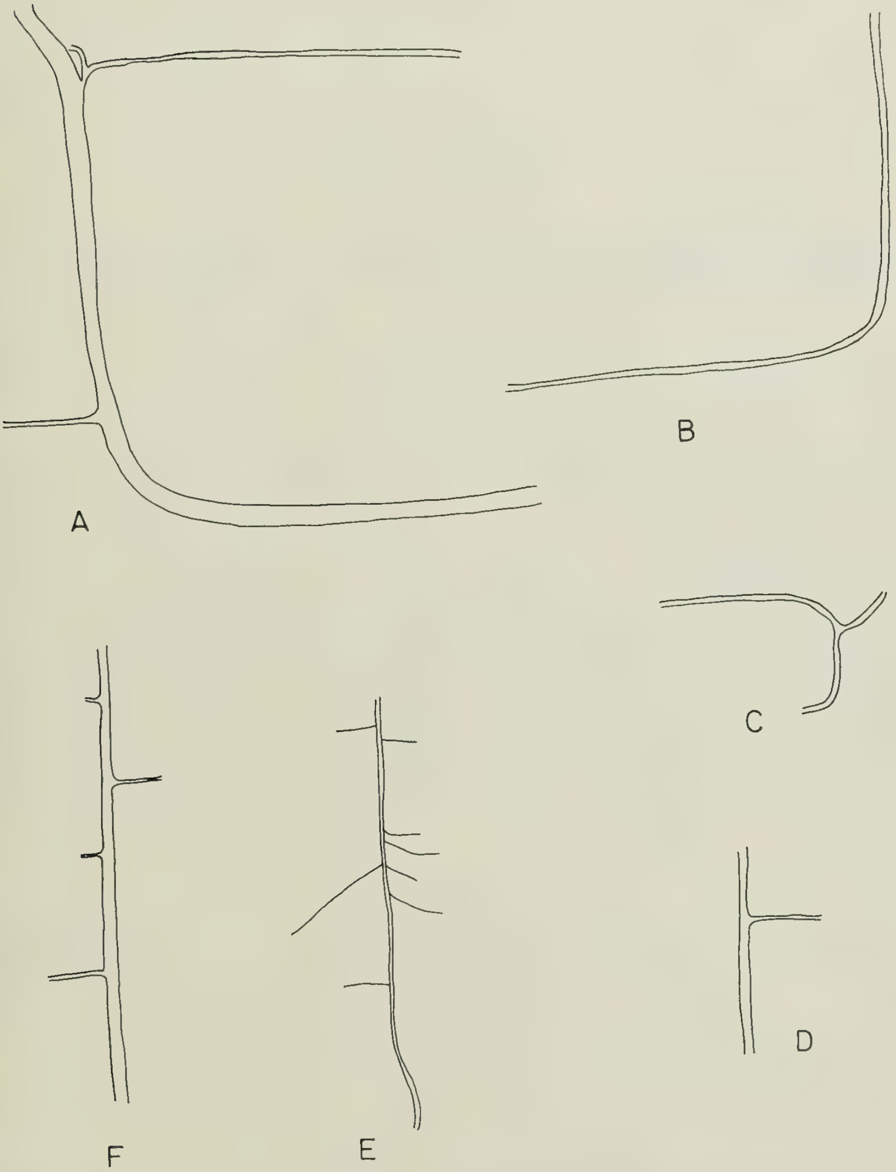


FIG. 7. Burrow type C. A–D, Lower Chalk, Middle Cenomanian; Glynde, Sussex. E–F, Lower Chalk, Upper Cenomanian; Dorking, Surrey. All specimens in relief on vertical solution planes. All × $\frac{1}{4}$.

which they branch off at right angles. Some of these burrows curve round to a horizontal position and have tunnels 10–25 cm. long.

Discussion. Burrows of this type are best seen on vertical solution planes, where they frequently stand out in relief. From their abundance on such surfaces they are clearly responsible for much of the sedimentary mottling seen in the Lower Chalk.

Some fragments compare with *Lennea* Kräusel & Weyland (1932, 1934, Paulus 1957, Häntzschel 1962, 1965) from the Devonian of Germany, but are generally smaller and lack the diagnostic bifurcation of the lateral tunnels.

It would seem reasonable to regard this form of burrow as produced by worms or some worm-like animal.

Occurrence. Present in all sections in the Lower Chalk examined, particularly in the upper part where they are prominent on vertical solution planes.

Burrow Type D

(Pl. 5, fig. 4; Pl. 7, figs. 1, 4, 5; Pl. 9, fig. 5)

1897 *Terebella lewesiensis* (Mantell); Davies : 145–148 (pars.).
1911 " *Terebella* " *cancellata* Bather : 551–553 (pars.), pl. 24, fig. 5 only.

Description. Vertical and horizontal cylindrical burrows, straight or slightly sinuous, unbranched so far as is known, between 5 and 25 mm. in diameter. Fragments only known, up to 20 cm. long. Surface covered in long, fine, straight or slightly spiral longitudinal ridges, also bearing coarser longitudinal folds.

Discussion. As already noted, material described by Bather (1911) as " *Terebella* " *cancellata* includes two distinct forms. The forms considered here are those bearing fine longitudinal ridges, interpreted by Bather (p. 552) as follows: " It seems quite certain that these fossils represent tubes, which lay on the sea-floor or in the semi-floating ooze of which it consisted, and, either being deserted by the creature that formed them or persisting after its death and decay, were filled with the ooze in which they lay. The tube wall it is clear, was of such strength and consistency as to retain its form fairly well during this process, and yet of such composition that it disappeared after the partial consolidation of the ooze. The markings on the infilling of the tube may be due to two causes; either a similar folding of the tube-wall during life or a wrinkling and contraction of the tube after death and perhaps even after burial. . . . the irregularity and variable development of the folds suggest that they, at least, were due to post-mortem change ".

My own view is that these are burrows, and that they never existed as free tubes on the surface.

The surface features of these burrows can be interpreted as the result of two different processes. The fine ridges, I would interpret as the result of some worm-like animal passing through sediment, the ridges arising from bristles or appendages, or even grains of sediment stuck on the body. The longitudinal folds have a quite different origin and appear to be post-depositional compaction effects.

Clearly, there is no similarity to the reticulate surface ornamentation of the holotype of " *Terebella* " *cancellata*.

A rather similar ornamentation is present on the " fucoids " *Gyrolithes dewalquei* Saporta (Saporta 1884) *Codites neocomiensis* Saporta & Meunieur (Saporta 1882) and *Cylindrites rimosus* Heer (Heer 1877).

OCCURRENCE. Common in all sections examined in the Weald, Isle of Wight and Chilterns.

BURROW TYPE E

(Pl. 2, fig. 3)

DESCRIPTION. Cylindrical burrows, generally 1–2 cm. in diameter, known only from unbranched fragments. Sections show the filling of these burrows is septate, being made up of meniscus-shaped laminae.

INTERPRETATION. Burrow-fillings showing this type of lamination can be produced by a number of groups. *Thalassinoides* occasionally show this type of filling, as do other undoubted crustacean burrows, such as *Ophiomorpha*. The same type of structure can be produced by coelenterates (Schaefer 1962 : 326, fig. 165), echinoids (Schaefer 1962 : 348, fig. 183) and some bivalves (Schaefer : 424, fig. 223). Under the conditions of chalk sedimentation, and by comparison with other forms, these are probably crustacean burrows.

OCCURRENCE. Uncommon in all sections of the Lower Chalk examined.

Many other trace fossils are represented in the Lower Chalk. " *Terebella* " *lewesiensis* (Mantell), worm tubes lined with fish, plant or echinoderm debris should be interpreted as trace fossils, as should the micro-coprolites described by Wilcox (1953) from the Upper Chalk, which also occur in the Lower. Borings, in shells, pebbles and rock surfaces are very abundant. In addition to species of *Cliona*, other sponge borings (*Filuroda*), algal and fungal perforations (*Calcidelectrix*, *Dictyoporus*), cirripede bores (*Zapfella*, *Rogerella*), bryozoan borings and bivalve crypts all occur.

VI. CONCLUSIONS

The activities of burrowing organisms are shown to be universally present in the Lower Chalk. The most obvious are those of crustaceans (*Thalassinoides*, *Spongeliomorpha*) and " worms " (*Chondrites*). Several poorly known burrows are also described. Of previously described assemblages, the present one compares best with the Lower Lias (Hallam 1961), where both *Chondrites* and *Thalassinoides* occur. U-shaped burrows (*Rhizocorallium* etc.), common in the Lower Lias, are, however, absent in the Chalk.

A problem of the Lower Chalk fauna, in view of the abundance of burrows, is the absence or great rarity of the animals responsible. With worms, disappearance of the soft body is readily understood, but the absence of crustaceans demands explanation. The crustacean fauna of the Lower Chalk is very limited. By far the most abundant form is the large, lobster-like *Enoploclytia,* though the very massive claws and thick, thorny carapace suggest that it did not burrow. The only other macrurous crustacean I have seen is *Glyphea willeti* (Woodward), which, in view of the thin, rather delicate exoskeleton, could well have burrowed. In size, it would fit some of the larger *Thalassinoides,* but it is rare. Callianassids, recorded in association with *Thalassinoides* elsewhere, appear to be totally absent from the Lower Chalk facies of the Cenomanian, although a " *Callianassa* " sp. is present in division A of the Cenomanian Limestone of S. Devon. Hume (1897) records a *Callianassa* sp. as occurring commonly in the Upper Glauconitic Beds (Cenomanian) at Colin Glen, Co. Antrim. Callianassids also occur in the Upper Greensand of the Devon Coast (matrix of museum specimens suggests the Top Sandstones) and the Gault.

Brachyurous crustaceans are equally rare; a few specimens of *Diaulax* and *Necrocarcinus* are known from the Lower Chalk, whilst crabs are not uncommon in the sandy facies of the Cenomanian, particularly at Wilmington. In all, the known crustacean remains give few clues to the identity of the burrowers. A possible explanation of absence is suggested by recent burrowing forms which have a thin, sometimes even transparent exoskeleton, very poorly calcified. Sloughs are generally removed from burrows, whilst moribund individuals leave their burrows prior to death.

Under these conditions it seems possible that on the Lower Chalk sea floor the organically-rich remains were completely eaten or destroyed by scavengers and micro-organisms prior to burial.

VII. ACKNOWLEDGMENTS

I am grateful to Dr. J. M. Hancock and Dr. J. D. Taylor for reading the manuscript of this paper and for making many helpful suggestions. I have profited from discussions with Dr. R. Bromley, Dr. C. V. Jeans, Dr. R. P. S. Jefferies and many others; Mr. P. Palmer kindly provided me with photographs of the types of *Terebella cancellata* and *T. harefieldensis*; Mr. R. Cleevely has aided me greatly in finding some of the more obscure literature. Dr. H. W. Ball, Mr. S. Ware and Dr. C. L. Forbes have kindly allowed me to examine material in their care, whilst Dr. Jefferies has generously allowed me to work on his collection, now in the Sedgwick Museum. Mr. B. McWilliams of the Norwich Castle Museum searched the collections for type material of *T. paradoxica*. Preparation of illustrations by the Technical Staff of King's College, under the direction of Mr. E. O. Rowlands is acknowledged, particularly the assistance of Miss M. Baker in preparation of the plates. I am deeply grateful to my parents for their encouragement and assistance.

Part of the work was carried out under the tenure of a N.E.R.C. grant, which is gratefully acknowledged.

VIII. REFERENCES

Abel, O. 1935. *Vorzeitliche Lebensspuren.* 644 pp., 530 figs. Jena.

Andert, H. 1934. Die Kreideablagerungen zwischen Elbe und Jeschken. III. Die Fauna der Obersten Kreide in Sachsen, Böhmen und Schlesien. *Abh. preuss. geol. Landesanst.,* Berlin, **159** : 1–477, pls. 1–21.

Andrews, H. N. 1955. Index of Generic Names of Fossil Plants 1820–1950. *Bull. U.S. Geol. Surv.*, Washington, **1013** : 1–262.

Arkell, W. J. 1935. The Portland Beds of the Dorset Mainland. *Proc. Geol. Assoc.*, London, **46** : 301–347, pls. 19–26.

Barrois, C. 1882. Recherches sur les terrains anciens des Asturies et de la Galicie. *Mém. Soc. Géol. Nord*, Lille, **2** : 1–630, pls. 1–20.

Bather, F. A. 1911. Upper Cretaceous Terebelloids from England. *Geol. Mag.*, London (5) **8** : 481–487, 549–556, pl. 24.

Billinghurst, S. A. 1927. On some New Ammonoidea from the Chalk Rock. *Geol. Mag.*, London, **64** : 511–518, pl. 16.

Black, M. 1953. The Constitution of the Chalk. *Proc. geol. Soc. Lond.*, **1499** : 81–86.

Black, M. & Barnes, B. 1959. The Structure of Coccoliths from the English Chalk. *Geol. Mag.*, London, **96** : 321–328, pls. 8–12.

Blake, J. F. & Hudleston, W. H. 1877. On the Corallian Rocks of England. *Quart. Jl. geol. Soc. Lond.*, **33** : 260–405, pls. 12–17.

Burnaby, T. P. 1962. The Palaeoecology of the Foraminifera of the Chalk Marl. *Palaeontology*, London, **4** : 599–608.

Cayeux, L. 1897. Contribution à l'étude micrographique des terrains sédimentaires. II. Craie du Bassin de Paris. *Mém. Soc. Géol. Nord*, Lille, **4** : 206–563, pls. 9, 10.

Dales, R. P. 1957. Interrelations of organisms. A. Commensalism. *In* Hedgepeth, J. W. (Ed.) *Treatise on Marine Ecology and Palaeoecology*, **1**, Ecology *Mem. Geol. Soc. Amer.*, **67** : 391–412, pl. 1.

Darder, B. 1945. Estudio geológico del Sur de la Provincia de Valencia y Norte de la de Alicante. *Bol. Inst. Min. Geol. España*, Madrid, **57** : 59–362, pls. 1–11.

Davidson, C. 1891. On the amount of sand brought up by Lobworms to the surface. *Geol. Mag.*, London (3) **8** : 489–493.

Davies, W. 1879. On some Fish Exuviae from the Chalk, generally referred to *Dercetis elongatus*, Ag.: and on a New Species of Fossil Annelide, *Terebella Lewesiensis*. *Geol. Mag.*, London (2) **6** : 145–148.

Dettmer, F. 1912. *Spongites saxonicus* Geinitz und die Fucoidenfrage. *Neues Jb. Min. Geol. Paläont.*, Stuttgart, **1912** : 114–126, pls. 8, 9.

—— 1914. Die *Spongites-saxonicus*—Frage. *Sitz.-Ber. u. Abh. naturwiss. Gesellsch. ' Isis '*, Dresden, **1913** : 50–54.

—— 1915. Neus zum Fucoidenproblem. *Centralbl. Min. Geol. Pal.*, Stuttgart, **1915** : 285–287, 1 fig.

Ehrenberg, K. 1938. Bauten von Decapoden (*Callianassa* sp.) aus dem Miozän (Burdigal) bei Eggenburg im Gau Nieder-Donau (Niederösterreich). *Paläont. Z.*, Berlin, **20** : 263–284, pls. 27–29.

—— 1944. Ergänzende Bemerkungen zu den seinerzeit aus dem Miozän von Burgschleinitz beschriebenen Gangkernen und Bauten dekapoder Krebse. *Paläont. Z.*, Berlin, **23** : 354–359.

Eichwald, E. d' 1865. *Lethaea Rossica* **2**, 1, *Periode Moyenne*. 640 pp. Stuttgart.

Ellenberger, F. 1946. Observations nouvelles sur la craie jaune à tubulures de Meudon. *C.R. Soc. Géol. Fr.*, Paris, **1946**, 11 : 202–204.

—— 1947. Le problème lithologique de la craie de Meudon. *Bull. Soc. Géol. Fr.*, Paris (5) **17** : 255–274.

Esper, E. J. C. 1799. *Die Pflanzenthiere.* In *Abbildungen nach der Natur mit Farben erleuchtet nebst Beschreibungen*, **2**, 12 : 221–304, pls. Nuremberg.

Farrow, G. E. 1966. Bathymetric zonation of Jurassic trace fossils from the coast of Yorkshire, England. *Palaeogeography, Palaeoclimatol., Palaeoecol.*, **2** : 103–151, pls. 1–7.

Felix, J. 1913. Über ein cretaceisches Geschiebe mit *Rhizocorallium Gläseli* n. sp. aus dem Diluvium bei Leipzig. *Sitz.-Ber. naturf. Ges. Leipzig*, **39** : 19–25, 37, pl. 1.

Ferguson, L. 1965. A note on the emplacement of sediment in the trace-fossil *Chondrites*. *Proc. geol. Soc. Lond.*, **1622** : 79–82, fig. 1.

Fiege, K. 1944. Lebensspuren aus dem Muschelkalk Nordwestdeutschlands. *Neues Jb. Min., Geol., Paläont.*, Stuttgart (B) **88** : 401–426, 6 figs.

Fisher, W. K. & MacGinitie, G. E. 1928. The natural history of an echiuroid worm. *Ann. Mag. Nat. Hist.*, London (10) **1** : 204–213, pl. 1.

Frič, A. 1878. Studien im Gebiete der böhmischen Kreideformation. II. Die Weissenberger und Malnitzer Schichten. *Arch. naturw.Landesdurchf. Böhm.*, Prague, **4**, 1 : 1–151.

Geinitz, H. B. 1839–42. *Charakteristik der Schichten und Petrefacten des sächsisch-böhmischen Kreidegebirges.* 116 pp., 24 pls. Dresden & Leipzig.

—— 1871–75. Das Elbthalgebirge in Sachsen. *Palaeontographica*, Stuttgart, **20** : 1–319, pls. 1–67.

Gignoux, M. 1926. *Géologie Stratigraphique.* vi + 588 pp., 124 figs. Paris.

Glaessner, M. F. 1947. Decapod Crustacea (Callianassidae) from the Eocene of Victoria. *Proc. R. Soc. Vict.*, Melbourne, **59** : 1–7, pls. 1, 2.

Gmelin, J. F. 1793. *C. a. Linne . . . Systema Naturae . . . Editio decima tertia aucta reformata cura J. F. Gmelin*, **3**. 476 pp., 3 pls. Lipsiae.

Goeppert, H. R. 1842. Über die fossile Flora der Quadersandsteinformation in Schlesien, als erster Beitrag zur Flora der Tertiärgebilde. *Nova Acta Caes. Leop.–Carol.*, Breslau & Bonn, **19**, 2 : 97–134, pls. 46–53.

—— 1847. Zur Flora des Quadersandsteins in Schlesien als Nachtrag zu der früher erschienenen Abhandlung über denselben Gegenstand. *Nova Acta Caes. Leop.–Carol.*, Breslau & Bonn, **22**, 1 : 356–365, pls. 35–38.

—— 1854. Quadersandsteinformation insbesondere über *Cylindrites spongioides* m. *Verh. nat. Ver. preuss. Rheinlande u. Westph.* (n.f.) **11** : 229–234, pl. 3.

Hallam, A. 1961. A sedimentary and faunal study of the Blue Lias of Dorset and Glamorgan. *Phil. Trans. R. Soc.*, London (B) **243** : 1–44, pls.

Hancock, J. M. 1963. The hardness of the Irish Chalk. *Irish Nat. J.*, Belfast, **14** : 157–164.

Häntzschel, W. 1934. Schraubenförmige und spiralige Grabgänge in turonen Sandsteinen des Zittauer Gebirges. *Senckenbergiana*, Frankfurt am Main, **16** : 313–324, 4 figs.

—— 1935. *Xenohelix saxonica* n. sp. und ihre Deutung. *Senckenbergiana*, Frankfurt am Main, **17** : 105–108.

—— 1938. Quer–Gliederung bei *Littorina*-Fährten, ein Beitrag zur Deutung von *Keckia annulata* Glocker. *Senckenbergiana*, Frankfurt am Main, **20** : 297–304, 6 figs.

—— 1952. Die Lebensspuren von *Ophiomorpha* Lundgren im Miozän bei Hamburg, ihre weltweite Verbreitung und Synonymie. *Mitt. Geol. Staats inst. Hamburg*, **21** : 142–153, pls. 13, 14.

—— 1962. Trace fossils and Problematica. *Treatise on Invertebrate Paleontology*, Part W : 177–245, figs. 109–149. New York.

—— 1964. Spurenfossilien und Problematika im Campan von Beckum(Westf.). *Fortschr. Geol. Rheinl. Westf.*, Krefeld, **7** : 295–308.

—— 1965. *Fossilium Catalogus* 1 : Animalia, Pars. **108**, Vestigia Invertebratorum et Problematica. 140 + 2 pp. s' Gravenhage.

Heer, O. 1877. *Flora Fossilis Helvetiae. Die vorweltliche Flora der Schweiz.* 182 pp., 70 pls. Zürich.

Hester, S. W. 1965. Stratigraphy and Palaeogeography of the Woolwich and Reading beds. *Bull. Geol. Surv. G.B.*, London, **23** : 177–137, pl. 10.

Hughes, T. M. 1884. On the so-called *Spongia paradoxica* (S. Woodward) from the Red and White Chalk at Hunstanton. *Quart. Jl. geol. Soc. Lond.*, **40** : 273–279.

Hume, W. F. 1893. *Chemical and Micro-mineralogical Researches on the Upper Cretaceous Zones of the South of England.* 103 pp. London.

—— 1897. The Cretaceous Strata of County Antrim. *Quart. Jl. geol. Soc. Lond.*, **53** : 540–606, pls. 44, 45.

Jefferies, R. P. S. 1962. The Palaeoecology of the *Actinocamax plenus* subzone (Lowest Turonian) in the Anglo–Paris Basin. *Palaeontology*, London, **4** : 609–647, pls. 77–79.

Jefferies, R. P. S. 1963. The Stratigraphy of the *Actinocamax plenus* subzone (Turonian) in the Anglo–Paris Basin. *Proc. Geol. Ass.*, London, **74** : 1–33, pls. 1, 2.

Jukes-Brown, A. J. & Hill, W. 1900. The Cretaceous Rocks of Britain. Vol. I—Gault and Upper Greensand. *Mem. Geol. Surv. U.K.*, London. xiv + 499 pp., 5 pls.

—— 1903. The Cretaceous Rocks of Britain. Vol. 2.—The Lower and Middle Chalk of England. *Mem. Geol. Surv. U.K.*, London. xiii + 556 pp., 8 pls.

—— 1904. The Cretaceous Rocks of Britain. Vol. 3—The Upper Chalk of England. *Mem. Geol. Surv. U.K.*, London. x + 566 pp., pl. 9.

Keij, A. J. 1965. Miocene trace-fossils from Borneo. *Paläont. Z.*, Stuttgart, **39** : 220–228, pls. 28, 29.

Kennedy, W. J. 1967. Field meeting at Eastbourne, Sussex. *Proc. Geol. Ass.*, London, **77** : 365–370.

Kilpper, K. 1962. *Xenohelix* Mansfield 1927 aus der miozänen niederrheinischen Braunkohlenformation. *Paläont. Z.*, Stuttgart, **36** : 55–58, pl. 7.

Kräusel, R. & Weyland, H. 1932. Pflanzenreste aus dem Devon, II. *Senckenbergiana*, Frankfurt am Main, **14** : 185–190.

—— 1934. *Lennea schmidti*, eine pflanzenähnliche Tierspur aus dem Devon. *Paläont. Z.*, Berlin, **16** : 95–102, pls. 7–11.

Lambrecht, F. 1927. Schichtenfolge und Oberflächenformen im Winterberggebiete des Elbsandsteingebirges. *Mitt. Ver. Erdk.*, Dresden (N.F.) **1927** : 1–48.

Laubenfels, M. W. de 1955. Porifera : *Treatise on Invertebrate Paleontology*, Part E : 21–112, figs. 14–89. New York.

Lessertisseur, J. 1955. Traces fossiles d'activité animale et leur significance paléobiologique. *Mém. Soc. Géol. Fr.*, Paris (n.s.) **74** : 1–150, pls. 1–11.

MacGinitie, G. E. 1930. The Natural History of the Mud Shrimp *Upobegia pugettensis* Dana. *Ann. Mag. Nat. Hist.*, London (10) **6** : 36–44, pls. 1–3.

—— 1934. The Natural History of *Callianassa californiensis* Dana. *Amer. Midl. Nat.*, Notre Dame (Indiana), **15** : 166–177, pls. 5, 6.

Mantell, G. A. 1822. *The fossils of the South Downs.* 320 pp., 43 pls. London.

—— 1833. *The Geology of the South-East of England.* xix + viii + 415 pp., 7 pls. London.

Marlière, R. 1933. De nombreux bancs phosphatés dans la craie à *Actinocamax quadratus* du basin de Mons. *Ann. Soc. géol. Belg.*, Bruxelles, **56** : 289–301, pls. 1, 2.

Maubeuge, P. L. & Lanly, R. 1952. Sur un problématica du Bathonien moyen de la région de Neufchâteau. *Bull. Soc. Sci. Nancy*, **11** : 122–124, fig.

Mertin, H. 1941. Decapode Krebse aus dem subhercynen und Braunschweiger Emscher und Untersenon sowie Bemerkungen über einige verwandte Formen in der Oberkreide. *Nova Acta Leop.–Carol.*, Halle (Saale), **10**, 68 : 149–262, pls. 1–8.

Meunier, S. 1889. Sur La *Spongeliomorpha saportai* espéce nouvelle parisienne *C.R. Acad. Sci. Paris*, **109** : 536–537.

Moore, H. B. 1932. Faecal pellets of the Anomuran Crustacea. *Proc. Roy. Soc. Edinb.*, **52** : 296–308.

—— 1939. Faecal pellets in relation to Marine deposits. *In* Trask, P. D., *Recent Marine Sediments, A symposium* : 516–524, fig. 1. Tulsa.

Oosting, C. H. 1925. Report on a collection of recent shells from Obi and Halmaher (Mollucas). *Meded. Landb. Hoogensch. Wageningen.*, **29** : 1–363.

Otto, E. v. 1852. *Additamente zur Flora des Quadergebirges in der Gegend um Dresden und Dippoldiswalde, enthaltend meist noch nicht oder wenig bekannte fossile Pflanzen.* 29 pp., 12 pls. Dippoldiswalde.

Paulus, B. 1957. Das Spurenfossil *Lennea schmidti* im Devon der Eifel. *Senckenberg. leth.*, Frankfurt am Main, **38** : 169–175, pl. 1.

Peake, N. B. & Hancock, J. M. 1961. The Upper Cretaceous of Norfolk. *Trans. Norfolk Norw. Nat. Soc.*, Norwich, **19** : 293–339, pl. 1.

Počta, P. 1885. Beiträge zur Kenntnis der Spongien der böhmischen Kreideformation. *Abh. böhm. Ges. Wiss.*, Prague, **3** : 1–40.

Pohl, M. E. 1946. Ecological Observations on *Callianassa major* Say at Beaufort, North Carolina. *Ecology*, Brooklyn, **27** : 71–80.

Prescher, H. 1954. Sedimentpetrographische Untersuchungen oberturoner Sandsteine im Elbsandsteingebirge. *Freiberger Forschungsh.*, C **11** : 1–96, 28 figs.

Pruvost, P. & Pringle, J. 1924. Excursion to the Boulonnais. *Proc. Geol. Ass.*, London, **35** : 56–67, pls. 5–7.

Purdy, E. G. 1964. Sediments as Substrates. *In* Imbrie, J. & Newell, J. *Approaches to Palaeoecology* : 238–271, 16 figs. New York.

Raciborski, M. 1890. *Taonurus ultimus* Sap. in Galizien. *Verh. k. k. geol. Reichsanst.*, Wien, **1890** : 265–266.

Reid, C. 1898. The Geology of the Country around Eastbourne. *Mem. Geol. Surv. U.K.*, London. iv + 15 pp., 18 figs.

Reis, O. M. 1910. Beobachtungen über Schichtenfolge und Gesteinsausbildungen in der fränkischen Trias. I. Muschelkalk und untere Lettenkohle. *Geognost. Jahresh.*, München, **22** : 1–258, pls. 1–11.

—— 1922. Über Bohrröhren in fossilen Schalen und über *Spongeliomorpha*. *Z. deutsch. geol. Ges.*, Berlin, **73** : 227–237, pl. 7.

Richter, P. B. 1909. *Beiträge zur Flora der unteren Kreide Quedlinburgs. Teil II. Die Gattung* Nathorstiana *P. Richter und* Cylindrites spongioides *Goeppert.* 12 pp., pls. 8–12. Leipzig.

Richter, R. 1947. *In* O. Wilkens, Palaontologische und geologische Ergebnisse der Reise von Kohl-Larsen (1928–29) nach Süd Georgien. *Abh. senckenberg. naturf. Ges.*, Frankfurt, **474** : 75, 9 pls.

Rieth, A. 1932. Neue Funde Spongeliomorpher Fucoiden aus dem Jura Schwabens. *Geol.-Paläont. Abh.*, Jena, **19** : 257–294, pls. 13–17.

Rios, J. M. & Hancock, J. M. 1961. Summer Field Meeting in the Spanish Pyrenees. *Proc. Geol. Ass.*, London, **72** : 373–390, pls. 15, 16.

Rose, C. B. 1835–6. A sketch of the Geology of West Norfolk. *Phil. Mag.*, London (3) **7** : 171–182, 274–279, 370–376; **8** : 28–42.

Saporta, G. de 1882. *A propos des algues fossiles.* 82 pp., 9 pls. Paris.

—— 1884. *Les organismes problématiques des anciennes mers.* 100 pp., 13 pls. Paris.

—— 1887. Nouveaux documents relatifs aux organismes problématiques des anciennes mers. *Bull. Soc. Géol. Fr.*, Paris (3) **15** : 286–302, pls. 3–7.

Schaefer, W. 1962. *Aktuo-Paläontologie nach Studien in der Nordsee.* 666 pp., 36 pls. Frankfurt am Main.

Schlotheim, E. F. Baron v. 1820. *Die Petrefactenkunde auf ihrem jetzigen Standpunkte durch die Beschreibung seiner Sammlung versteinerter und fossiler Überreste des Thier-und Pflanzenreiches der Vorwelt erläutert.* 437 pp., 15 pls. Gotha.

Schroeder, H. & Boehm, J., 1909. Geologie und Paläontologie der Subhercynen Kreidemulde. *Abh. preuss. geol. Landesanst., Berlin* (n.f.) **56** : 1–64, pls. 1–16.

Schultze, C. F. 1760. *Betrachtung der versteinerten Seesterne und ihrer Theile.* iv + 58 pp., 3 pls. Warsaw & Dresden.

Seeley, H. 1864. On the Hunstanton Red Rock. *Quart. Jl. geol. Soc. Lond.*, **20** : 327–332.

Seilacher, A. 1951. Der Röhrenbau von *Lanice conchilega* (Polychaeta). Ein Beitrag zur Deutung fossiler Lebensspuren. *Senckenbergiana*, Frankfurt am Main., **32** : 267–280.

—— 1955. Spuren und Lebenweise der Trilobiten: Spuren und Fazies im Unterkambrium. *In* Schindewolf, O. H. & Seilacher, A., Beiträge zur Kenntnis des Kambriums in der Salt Range (Pakistan). *Akad. Wiss. Lit. Mainz. math.-nat. Kl.*, **10** : 86–143, pls. 16–27.

—— 1964. Biogenic sedimentary structures. *In* Imbrie, J. & Newell, D. *Approaches to Palaeoecology* : 296–316, 8 figs., 1 tab. New York.

Semenow, W. P. 1899. La Faune des dépôts crétacés de Mangychlak et de quelques autres localités de la province transcaspienne. *Trav. Soc. Imp. Nat. St. Pétersb.*, **28**, 5 (Géol., Min.) : 1–178, pls. 1–4.

SIMPSON, S. 1957. On the trace-fossil *Chondrites*. *Quart. Jl. geol. Soc. Lond.*, **112** : 475–499, pls. 21–24.

SORBY, H. C. 1861. On the organic origin of the so-called " Crystalloids " of the Chalk. *Ann. Mag. Nat. Hist.*, London (3) **8**, 193–200.

SOWERBY, J. DE C. 1823–25. *The Mineralogy Conchology of Great Britain; or coloured figures of those remains of Testaceous Animals or Shells, which have been preserved at various times, in the earth*, **5**, pls. 408–443 (1823), 444–485 (1824), 486–508 (1825). London.

STERNBERG, K. M. GRAF. V. 1833. *Versuch einer geognostisch-botanischen Darstellung der Flora der Vorwelt.* **5–6**. 80 pp. Leipzig & Prague.

STEVENS, B. A. 1928. Ecological observations on the Callianassidae of Puget Sound. *Ecology*, New York, **10** : 399–405.

TAYLOR, J. H. 1964. Some aspects of diagenesis. *Advmt. Sci., Lond.*, **18** : 417–436, 7 figs.

TAYLOR, R. 1823. Geological section at Hunstanton Cliff, Norfolk. *Phil. Mag.*, London, **61** : 81–83.

THOMEL, G. 1961. Sur la présence du genre *Schloenbachia* dans le Vraconien supérieur de Saint-Laurent de l' Escarène (Alpes-Maritimes). *C.R. Soc. Géol. Fr.*, Paris, **1961** : 37.

VERWEY, J. 1930. Einiges über die Biologie ost-indischer Mangrovekrabben. *Treubia*, Buitenzorg, Bogor, **12** : 167–261, pls. 6–14.

WATELET, A. 1866. *Description des plantes fossiles du basin de Paris.* iv + 264 pp., Atlas 30 pp., 60 pls. Paris.

WEBSTER, T. 1814. On some new varieties of fossil Alcyonia. *Trans. geol. Soc., Lond.* : 371–387, pls. 27–29.

WEIGELT, J. 1929. Fossile Grabschächte brachyurer Decapoden als Lokalgeschiebe in Pommern und das *Rhizocorallium*-Problem. *Z. Geschiebforsch.*, Berlin, **5** : 1–42, pls. 1–4.

WEIMER, R. J. & HOYT, J. H. 1964. Burrows of *Callianassa major* Say, geologic indicators of littoral and shallow neritic environments. *J. Paleont.*, Tulsa, **38** : 761–767, pls. 123, 124.

WHITAKER, W. & JUKES-BROWNE, A. J. 1899. The Geology of the Borders of the Wash: including Boston and Hunstanton. *Mem. Geol. Surv. U.K.*, London. iv + 146 pp.

WHITE, E. I. 1923. Notes on a new Species of Terebelloid and other Phenomena in the Great Pit at Harefield, Middlesex, etc. *Proc. Geol. Ass.*, London, **34** : 43–46.

WILCOX, N. R. 1953. Some coprolites from phosphatic chalks in S.E. England. *Ann. Mag. Nat. Hist.*, London (12) **6** : 369–375, pl. 11.

WILSON, V. 1949. The Lower Corallian Rocks of the Yorkshire Coast and Hackness Hills. *Proc. Geol. Ass.*, London, **60** : 235–271, pls. 9, 10.

WILTSHIRE, T. 1859. On the Red Chalk of England. *Geologist*, London, **2** : 261–278 and *Geol. Ass. Spec. Papers*, **1859** : 1–18, pls. 1–4.

—— 1869. On the Red Chalk of Hunstanton. *Quart. Jl. geol. Soc. Lond.*, **25** : 185–192.

WOOD, C. J. 1965. Field Meeting on the Lower Chalk between Folkestone and Dover. *Proc. Geol. Ass.*, London, **76** : 301–304.

WOODWARD, S. 1830 *A synoptic table of British Organic remains.* xiii + 50 pp., 1 pl. London & Norwich.

—— 1833. *An Outline of The Geology of Norfolk.* 54 + 1 pp., 6 pls. Norwich.

ZARECZNY, S. W. 1878. O średnich warstwach kredowych w krakowskim okregu. *Krakow Kom. Fizyogr. Spraw.*, **12** : 176–246, pls. 4–8.

PLATE 1

Fig. 1. ***Thalassinoides saxonicus*** (Geinitz). Lower Chalk, Middle Cenomanian; Houghton Regis, near Dunstable, Beds. Base of a fallen block of Totternhoe Stone with part of the underlying Chalk Marl attached, the burrow is filled by Totternhoe Stone. Plan view, hammer head 16 cm. long.

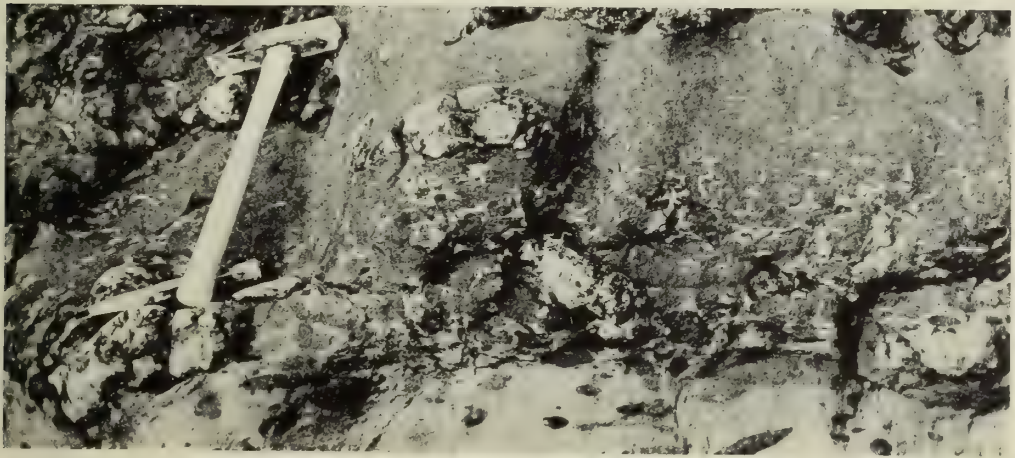
Fig. 2. ***Thalassinoides*** cf. ***suevicus*** (Rieth). Upper Greensand; Cow Gap, N.E. of Beachy Head, Eastbourne, Sussex. Burrow originates from the base of the Glauconitic Marl (Lower Cenomanian). Plan view, scale in inches.

Fig. 3. Burrows at base of the Glauconitic Marl, Lower Cenomanian; Compton Bay, Isle of Wight. Vertical section, hammer head 16 cm. long.

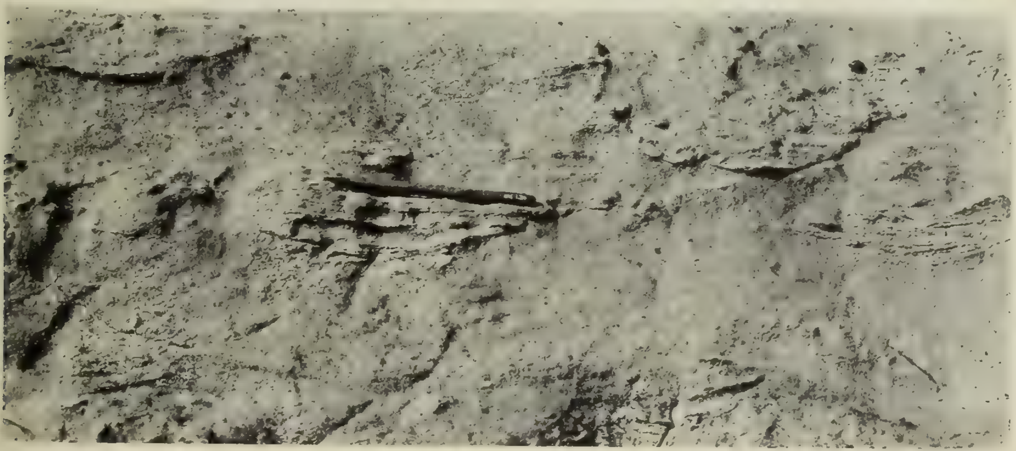
Fig. 4. Laminated structures. Lower Chalk, Middle Cenomanian, bed 7; foot of cliff 600 m. E. of Akers steps, Dover, Kent. Vertical section, pencil 9 cm. long.

1

2



3



4

PLATE 2

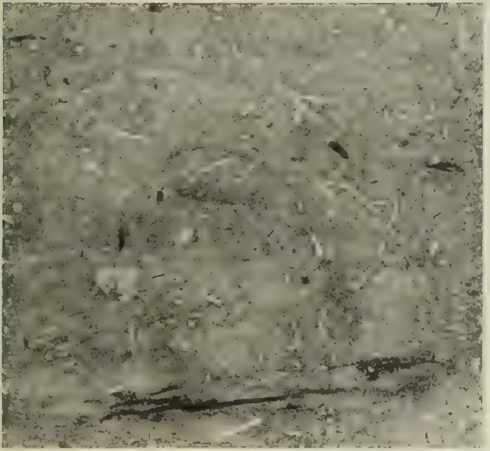
FIG. 1. ***Spongeliomorpha? annulatum*** ichnosp. nov. Glauconitic Marl, Lower Cenomanian; foreshore, East Wear Bay, Folkestone, Kent. Oblique section, hammer head 16 cm. long.

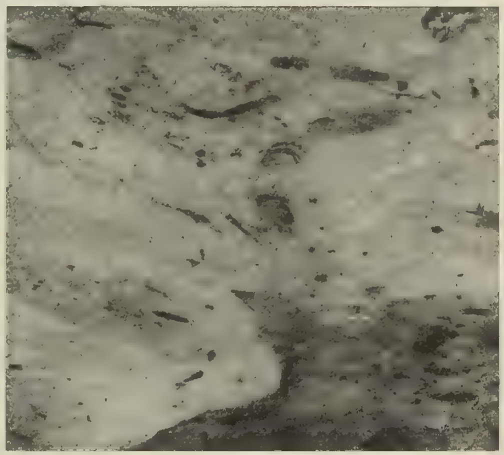
FIG. 2. Vertical section of burrowed chalk with abundant *Chondrites* sp. Lower Chalk, Upper Cenomanian; Betchworth Limeworks, Betchworth, Surrey. × 1.

FIG. 3. Vertical section of burrowed chalk with *Chondrites* sp. and burrow type E. Lower Chalk, Middle Cenomanian; Eastbourne, Sussex. × 1.

FIG. 4. Vertical section of burrowed chalk. Lower Chalk, Upper Cenomanian; Dover, Kent. Note relative abundance of *Chondrites* sp. in larger burrows. × 1.

1


2


3

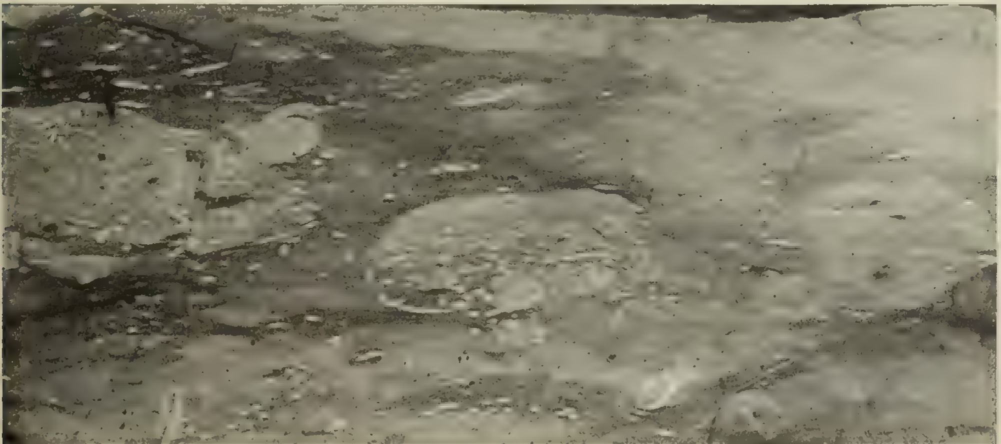

4

PLATE 3

Thalassinoides paradoxica (Woodward)

Neotype, B.M. (N.H.) T.545. Lower Chalk, Lower Cenomanian, *Paradoxica* bed; Hunstanton, Norfolk. Oblique view, scale in centimetres.

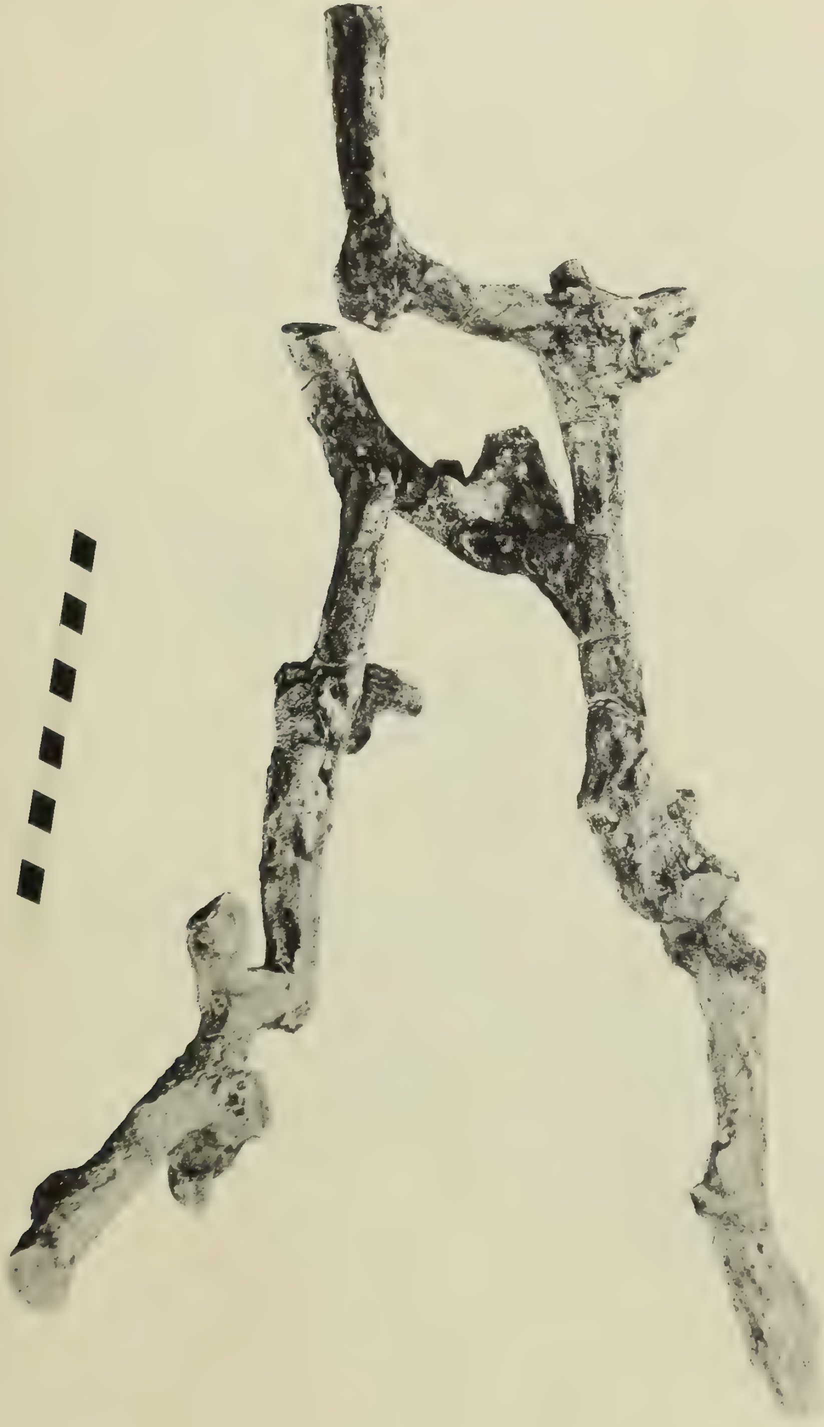


PLATE 4

Thalassinoides paradoxica (Woodward)

Neotype, B.M. (N.H.) T.545. Lower Chalk, Lower Cenomanian, *Paradoxica* bed; Hunstanton, Norfolk. Plan view, scale in centimetres.

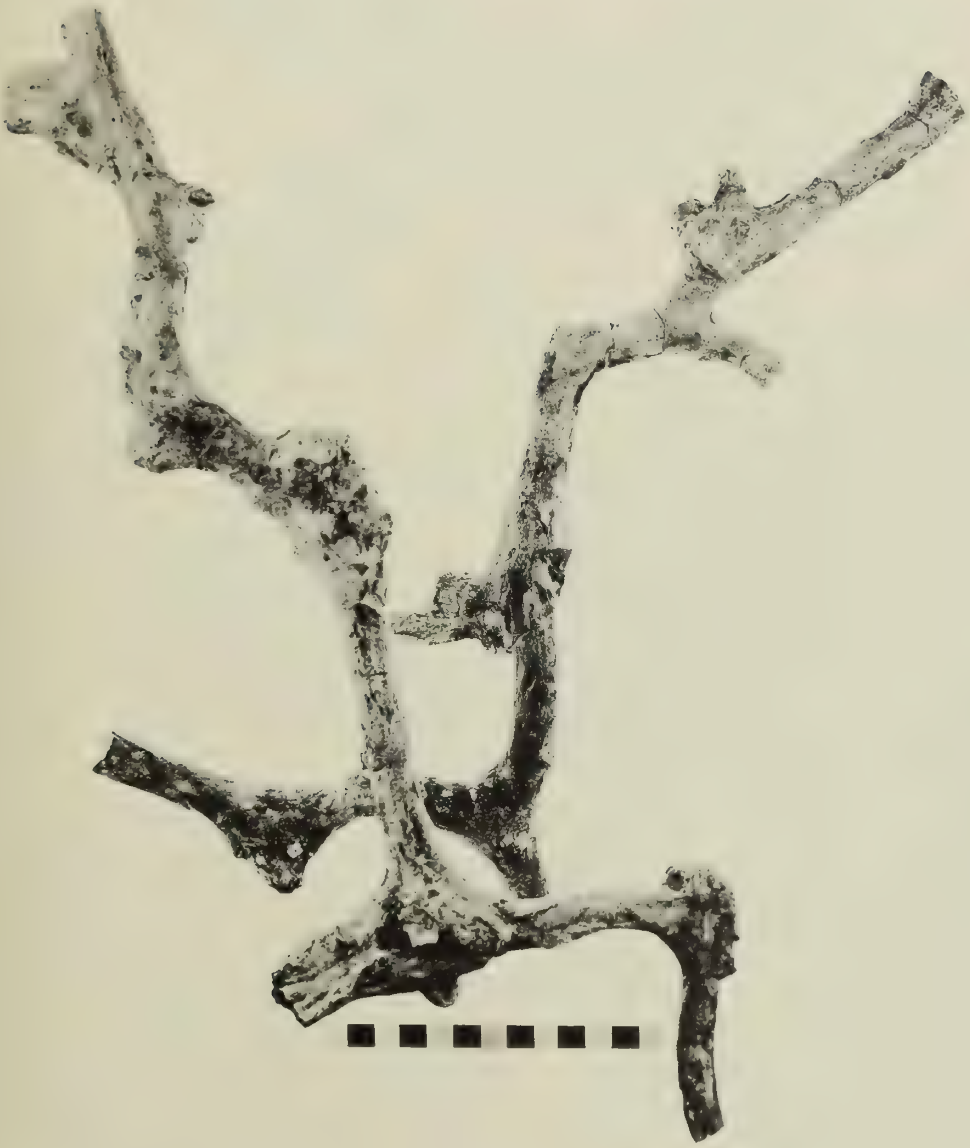


PLATE 5

FIG. 1. Laminated structure showing disruption of lamination by subsequent burrowing. B.M. (N.H.) T.550, Lower Chalk, Middle Cenomanian; Pit N.E. of Wouldham Hall, Wouldham, Kent. Vertical section, × 1. (Detail of Pl. 8, fig. 3).

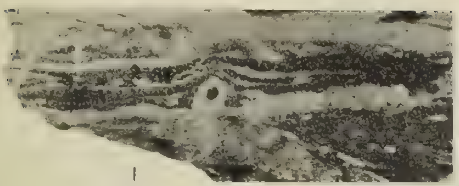
FIG. 2. ***Thalassinoides saxonicus*** (Geinitz). B.M.(N.H.) T.547, Lower Chalk, Middle Cenomanian, chalk beneath Totternhoe Stone; Houghton Regis, near Dunstable, Beds. Plan view of upper surface of termination showing ornamentation of elongate mounds. × $\frac{1}{2}$.

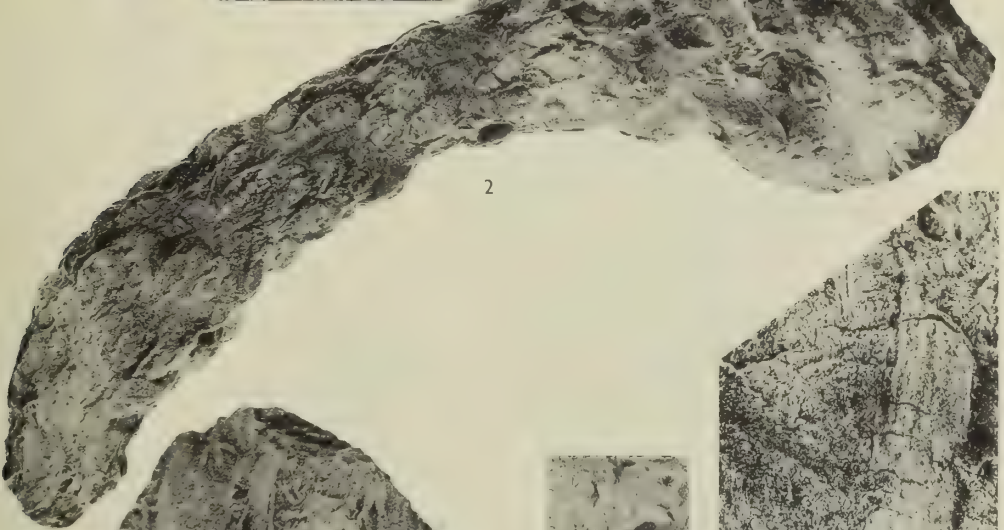
FIG. 3. ***Thalassinoides saxonicus*** (Geinitz). B.M.(N.H.) T.548. Same horizon and locality, detail of figured specimen (Pl. 6, fig. 3), showing bottom covered with *Chondrites* sp. × 1.

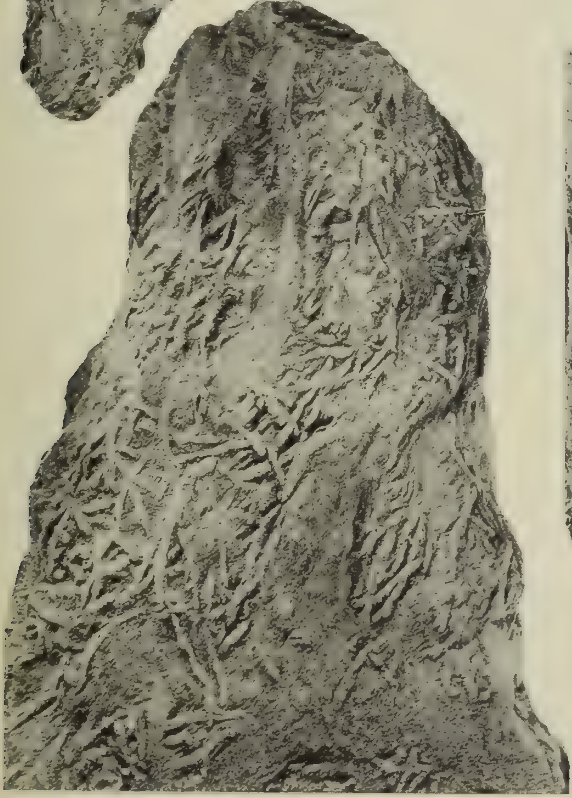
FIG. 4. Burrow type D. S.M.C. b92473 (Jefferies collection). *Plenus* Marls, bed i; Merstham, Surrey. × 1.

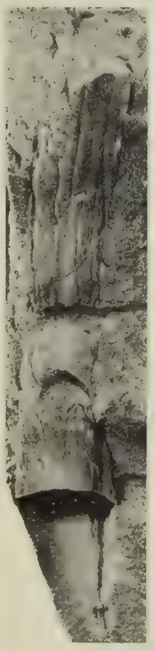
FIG. 5. ***Spongeliomorpha? annulatum*** ichnosp. nov. Holotype, B.M.(N.H.) T.554. Glauconitic Marl, Lower Cenomanian; section below Martello Tower no. 3, Copt Point, Folkestone, Kent. × 1.

All specimens except Fig. 1 coated with ammonium chloride.


1


2


3


4

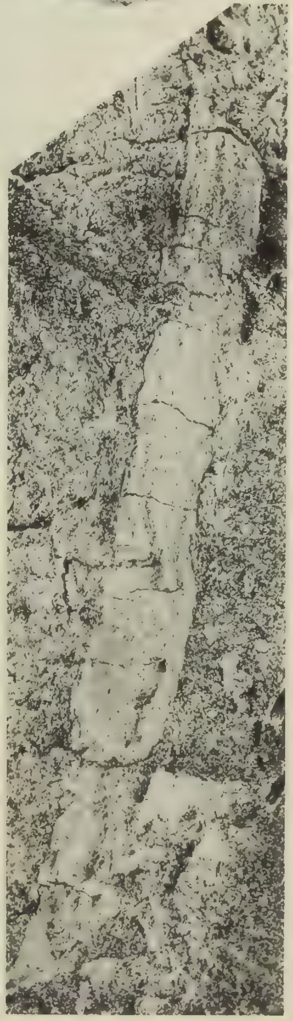

5

PLATE 6

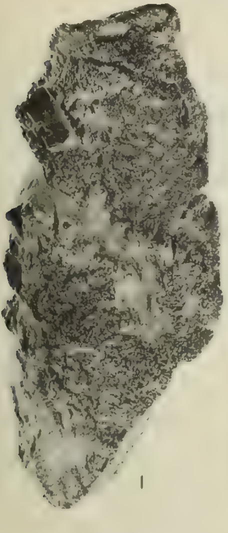
Fig. 1. ***Pseudobilobites jefferiesi*** ichnosp. nov. B.M. (N.H.) T.556. Lower Chalk, Upper Cenomanian; 7 m. below top of bed 8, base of Shakespeare Cliff; W. of Dover, Kent. Bottom surface, × 1.

Fig. 2. Cylindrical burrow full of coarse debris. S.M.C. B92827 (Jefferies collection). *Plenus* Marls, bed i; Merstham, Surrey. Listed by Jefferies (1963) as Problematicum sp. × 1.

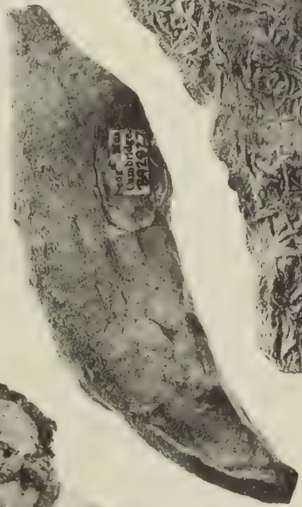
Fig. 3. ***Thalassinoides saxonicus*** (Geinitz). B.M.(N.H.) T.548. Lower Chalk, Middle Cenomanian, chalk beneath Totternhoe Stone; Houghton Regis, near Dunstable, Beds. Bottom surface of typical branching fragment covered with *Chondrites* sp. × 1.

Fig. 4. ***Thalassinoides ornatus*** ichnosp. nov. associated with ***T. saxonicus*** (Geinitz). Holotype B.M.(N.H.) T.559. Same horizon and locality. Top surface, × 1.

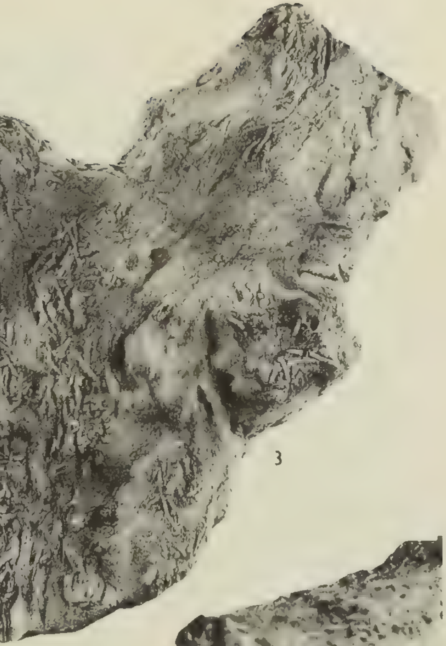
All specimens coated in ammonium chloride.



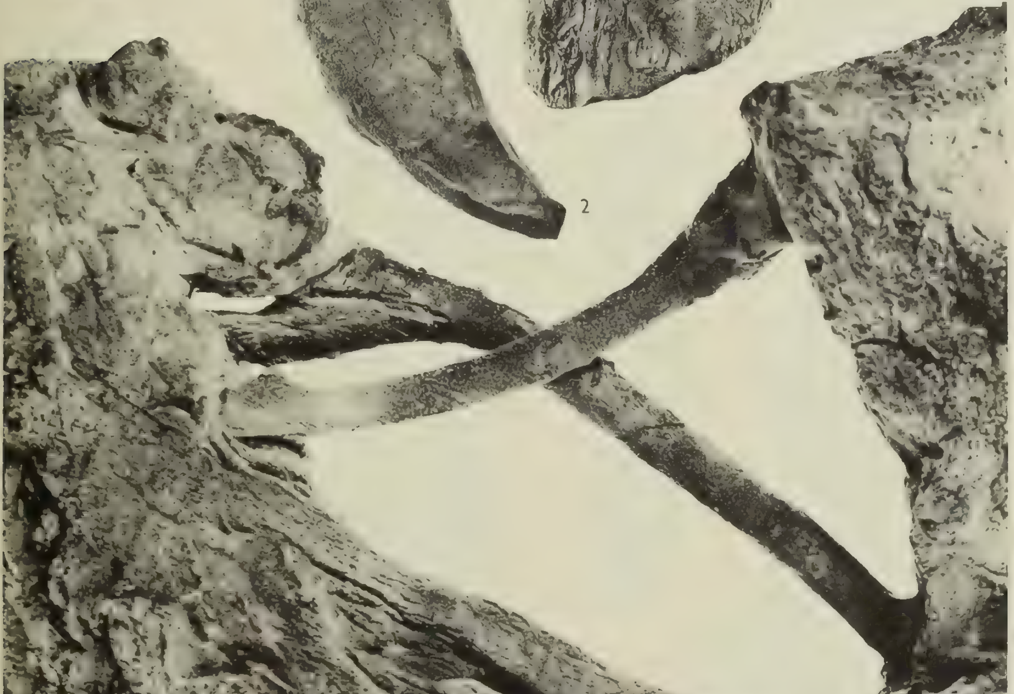
1


Cambridge
B9297

2



3



4

PLATE 7

FIG. 1. Burrow type D. B.M. (N.H.) T.557. Lower Chalk, Middle Cenomanian, horizon of abundant *Orbirhynchia mantelliana* (Sowerby) and *Sciponoceras baculoide* (Mantell); Beddingham Limeworks, Beddingham, near Glynde, Sussex. × 1.

FIG. 2. "***Terebella*" *harefieldensis*** White. Holotype, B.M.(N.H.) A.2445. Chalk/Reading Beds junction; The Great Pit, Harefield, Middlesex. × 1.

FIG. 3. ***Pseudobilobites jefferiesi*** ichnosp. nov. S.M.C. B91035. *Plenus* Marls, bed i; Merstham, Surrey. Figured Jefferies (1963, pl. 77, fig. 5). Bottom surface, × 1.

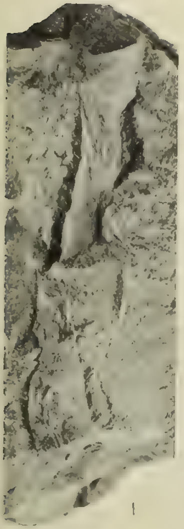
FIG. 4. Burrow type D. B.M.(N.H.) T.569, Lower Chalk, Middle Cenomanian; Bluebell Hill, Burham, Kent, × 1.

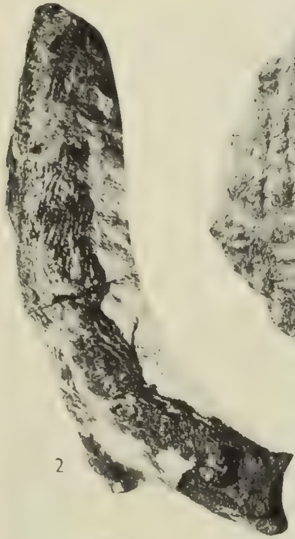
FIG. 5. Burrow type D. B.M.(N.H.) T.558, Lower Chalk, Middle Cenomanian; Glynde, Sussex. × 1.

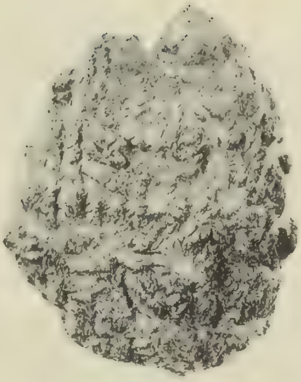
FIG. 6. ***Thalassinoides ornatus*** ichnosp. nov. Paratype, B.M.(N.H.) T.551. Lower Chalk, Middle Cenomanian, chalk below Totternhoe Stone; Houghton Regis, near Dunstable, Beds. × 1.

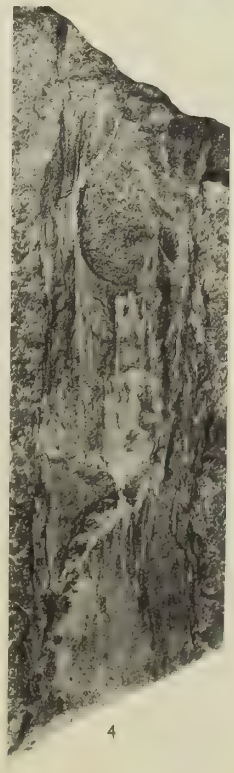
FIG. 7. ***Spongeliomorpha*** sp. B.M. (N.H.) T.553, same horizon and locality. × 1.

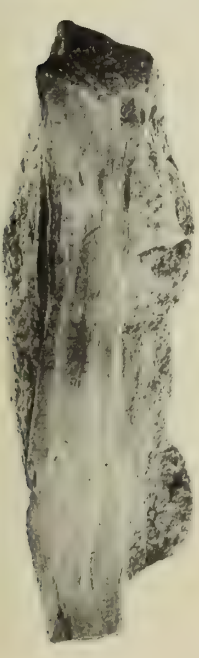
All specimens except Fig. 2 coated in ammonium chloride.

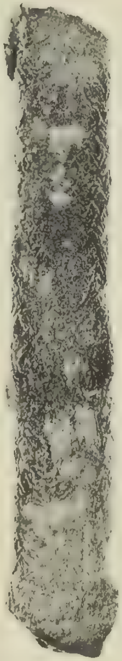

1


2


3


4


5


6

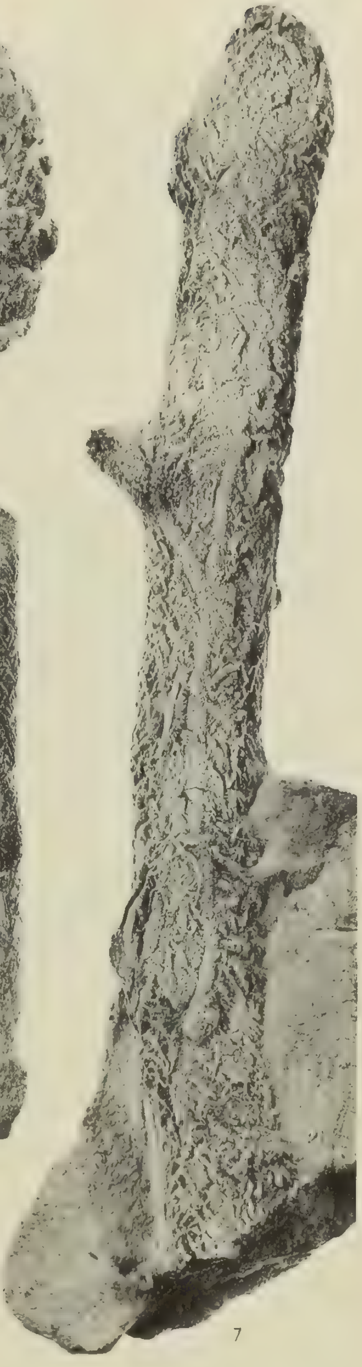

7

PLATE 8

Fig. 1. " ***Terebella*** " ***cancellata*** Bather. Holotype, B.M. (N.H.) 58253 (Capron collection). Lower Chalk, *subglobosus* Zone; Glynde, Sussex. Figured Bather (1911, pl. 24, fig. 3). × 1.

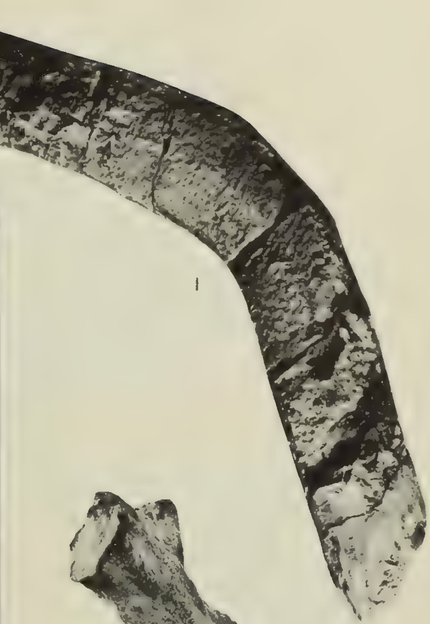
Fig. 2. " ***Terebella*** " ***cancellata*** Bather. Paratype, B.M. (N.H.) A.1574 (Capron collection). Lower Chalk; Cowslip pit, near Guildford, Surrey. × 1.

Fig. 3. Laminated structure. B.M. (N.H.) T.550, Lower Chalk, Middle Cenomanian; pit N.E. of Wouldham Hall, Wouldham, Kent. Vertical section, upper surface at left margin. $\times \frac{2}{3}$.

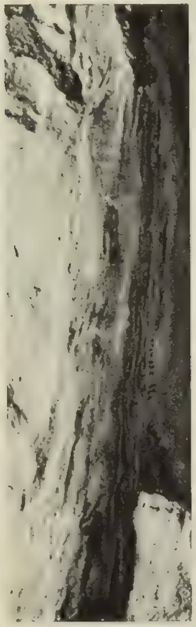
Fig. 4. ***Pseudobilobites jefferiesi*** ichnosp. nov. S.M.C. B91557 (Jefferies collection). *Plenus* Marls, bed i; Merstham, Surrey. Lower surface, × 1.

Fig. 5. ***Thalassinoides paradoxica*** (Woodward) B.M. (N.H.) T.549. Lower Chalk, Lower Cenomanian, *Paradoxica* bed; Hunstanton, Norfolk.

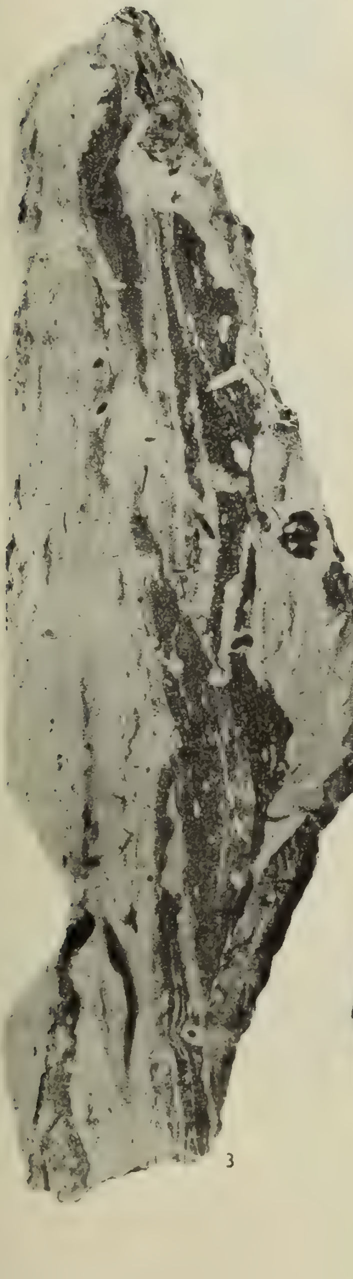
Figures 1–3 uncoated, 4, 5 coated with ammonium chloride.



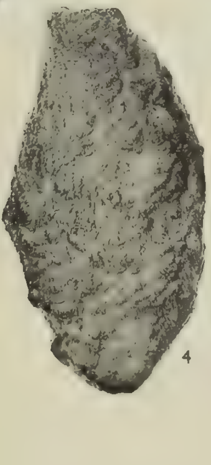
1



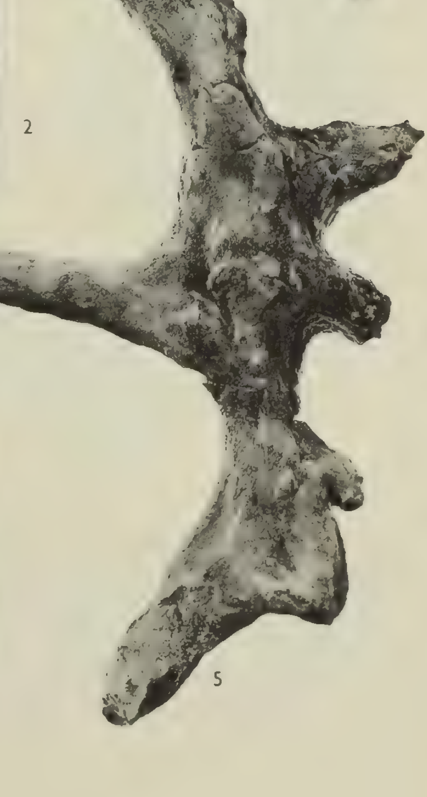
2



3



4



5

PLATE 9

FIG. 1. ***Chondrites*** sp. B.M. (N.H.) T.562. Lower Chalk, Middle Cenomanian, horizon of abundant *Orbirhynchia mantelliana* (Sowerby) and *Sciponoceras baculoide* (Mantell); 300 m. west of Head Ledge, N.E. of Beachy Head, Eastbourne, Sussex. × 1.

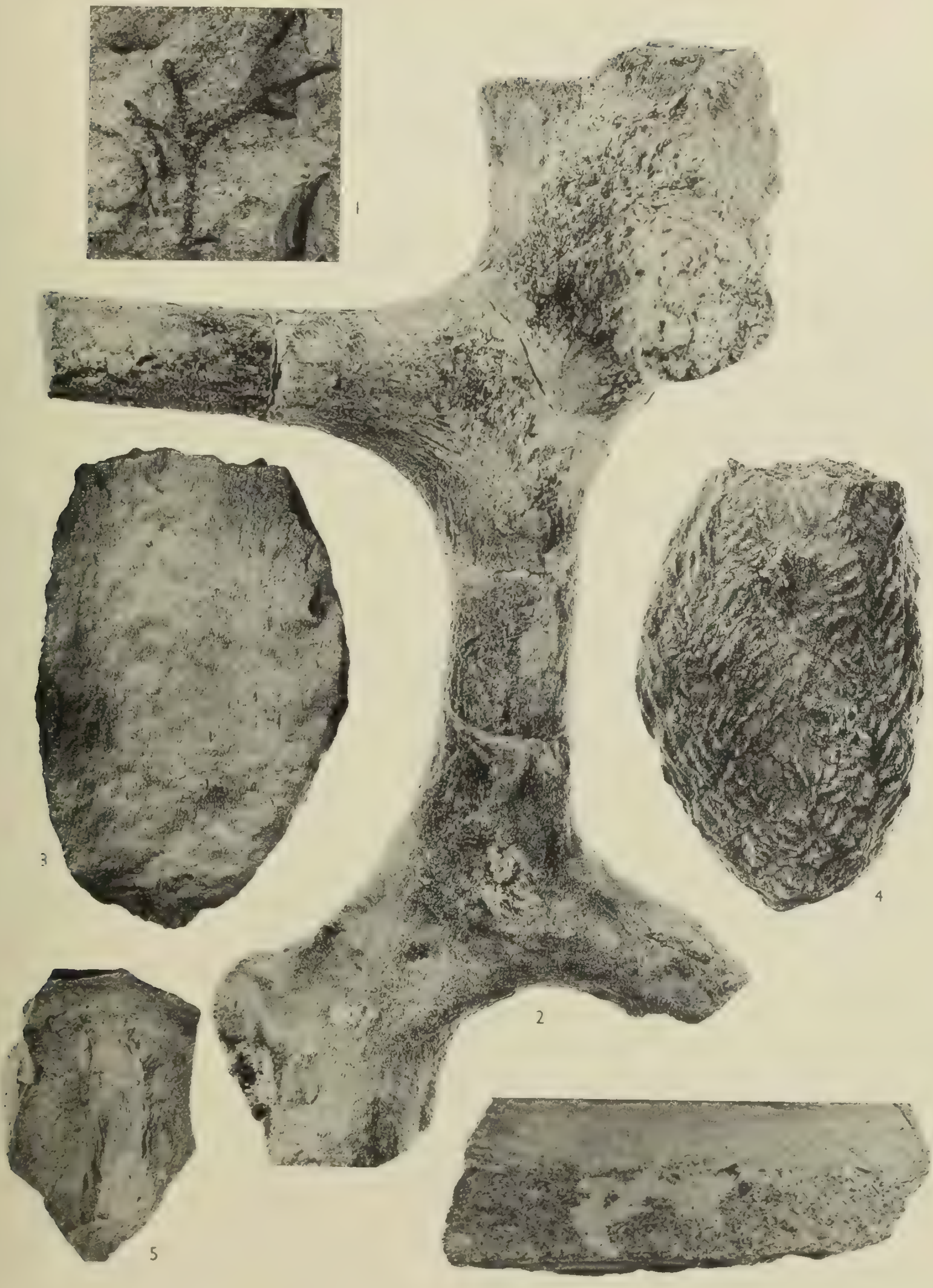
FIG. 2. ***Thalassinoides paradoxica*** (Woodward) B.M. (N.H.) T.546, Lower Chalk, Lower Cenomanian, Paradoxica bed; Hunstanton, Norfolk. × 1.

FIGS. 3, 4. ***Pseudobilobites jefferiesi*** ichnosp. nov. Holotype B.M. (N.H.). T.565. Lower Chalk, Middle Cenomanian, chalk below Totternhoe Stone; Pitstone, Buckinghamshire. 3, upper surface, 4, lower surface. × 1.

FIG. 5. Burrow type D. S.M.C. B92472 (Jefferies collection). *Plenus* Marls, bed i; Merstham, Surrey.

FIG. 6. ***Pseudobilobites jefferiesi*** ichnosp. nov. S.M.C. B91653b (Jefferies collection). *Plenus* Marls, bed 1; Lockinge, Berkshire.

All specimens except Figs. 1 and 6 coated with ammonium chloride.


1

2

3

4

5

6

BRITISH MUSEUM NATURAL HISTORY

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

A NEW *TEMPSKYA* FROM KENT

12 JAN

M. E. J. CHANDLER

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 4
LONDON: 1968

A NEW *TEMPSKYA* FROM KENT

12 JAN

BY

MARJORIE E. J. CHANDLER

Pp. 169–179; 12 *Plates*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 4
LONDON: 1968

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 15, *No.* 4 *of the Geological Palaeontological series. The abbreviated titles of the periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation
Bull. Br. Mus. nat. Hist. (Geol.).

© Trustees of the British Museum (Natural History) 1968

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 12 *January,* 1968 *Price* £1 10s

A NEW *TEMPSKYA* FROM KENT

By M. E. J. CHANDLER

MS accepted 18th April, 1967

SYNOPSIS

A silicified specimen with well-preserved cell structure, found on the shore at Sheppey, proves to be a new species of the Mesozoic " genus " *Tempskya* in which individual solenostelic stems are welded together into a " false stem " by their intertwining roots. Detailed morphology links this specimen most closely with *Tempskya grandis* from the Upper Cretaceous of Wyoming but the two are distinguished by the greater number of meristeles normally present within the rhizome section of the American species and the great difference of size.

The type of siliceous preservation suggests that the specimen may have come from the Woolwich Beds of Herne Bay.

The Kent *Tempskya* is only the second species to be recorded from England and is quite distinct from the well known *Tempskya erosa* found in the Wealden Beds and the Lower Greensand.

INTRODUCTION

SOME years ago a member of the United States Geological Survey, Dr. R. A. Scott, paid a visit to the Sheppey coast to see this famous source for London Clay plants. He picked up, lying loose on the shore, a somewhat waterworn " stem " and kindly gave it to the British Museum (Natural History). A transverse cut just below the apex of the specimen (V.51841) showed that it was a fern beautifully preserved in silica with excellent cell structure. The siliceous preservation raised the question of the origin of this plant so unlike the London Clay fruits and seeds which are commonly pyritized, occasionally carbonaceous or with calcitic internal casts and not infrequently a mixture of pyrites and carbonaceous tissues. The specimen has now been studied and the results of the investigations are described below.

DESCRIPTION OF SPECIMEN

The silicified " false stem " was originally about 12·5–13 cm. long. The cutting process when the apex was severed of course involved some loss of length. Both parts of the specimen have now been examined, further cuts have been made, and a few thin sections have been prepared. The specimen is now in four fragments. The poorly preserved basal part is numbered V.51841, the central part V.51841*a*; and the apex, which has further been cut longitudinally into two fragments, V.51841*b* and *c*. Of the six slides (V.51841*d–i*), V.51841*d* from the top of V.51841 is too ill-preserved to be very informative or worth thinning. V.51841*e* and *f* are from the upper surface of V.51841*a*, the slide *e* being lower than *f*. Slides V.51841 *g*, *h* and *i* come from the base of V.51841*b*. They do not extend across the whole breadth of the specimen nor even of the cut surface of V.51841*b*, but all three together with *b* 1 and 2 lie within about 10 mm. of the length of the " stem ".

The transverse diameter of the whole specimen at broadest (i.e. at about the middle) is 5.4 by 3.5 cm. In its rolled and waterworn state it shows superficially a complex of stems with general longitudinal alignment and some evidence of dichotomous bifurcation and intertwining, (Pl. 1, figs. 1, 2). Remains of a few projecting scattered petiole bases are seen (Pl. 1, fig. 2; Pl. 2, fig. 4). Section V.51841*f* passes through one stem in the early stages of dichotomous division (Pl. 1, fig. 3; Pl. 3, fig. 6; Pl. 4, fig. 7) so that there are two steles but both are still surrounded by a single cortex and epidermis which have become somewhat bilobed. The whole specimen is more abraded on one broad surface than on the other. Some crushing, dislocation and disintegration can be detected in the section towards this worn side making the structures more obscure here than elsewhere. There has been some disruption of the stele, for example, in the dividing stem (Pl. 3, fig. 6; Pl. 4, fig. 7). A few deep concavities show the surface view of ramentae in lighter coloured silica (Pl. 1, fig. 1). They are obscured by abundant freely branching roots many of which grew upwards. The fringed edges of the scales, due to their multi-cellular structure, show clearly in places. Despite wear and tear the specimen appears to retain, approximately at least, the original length and breadth, for emerging petiole bases project from the general surface both on the side and at the apex. The structure, at the lower end where amorphous silica has obliterated cell tissues, is more obscure than in the upper two-thirds of the specimen. More especially is this the case on the less well preserved side.

In transverse section in the upper part (Pl. 1, fig. 3) all or part of seven radially arranged dorsiventral stems are visible. They show a typical solenostelic structure. Five of them are closely adjacent to or actually at the circumference; two are more deeply embedded but still radially aligned. In all, the steles are towards the inner end of a radial line, and the leaf traces or meristeles at their outer ends. The spaces between the stems are packed closely with ramentae and roots of various sizes. The latter may be sectioned longitudinally for a short distance but are commonly transversely or obliquely cut in the slides and cut surfaces. The penetrating roots which pierce the scales and weave in and out weld the stems into the " false stem ". The solidity of the whole complex is undoubtedly enhanced by the process of silicification which unites stems, scales and roots into a solid inseparable mass, silica penetrating all tissues and replacing cell contents just as in *Osmunda dowkeri*.

The maximum transverse diameter of the component stems is about 15.5 by 9 mm., or 15 by 11 mm. in the middle of the specimen, larger, some 22 to 25 by 11 mm., in the basal part. Near the apex some stems are smaller, 12 or 13 by 8 mm., but others are 15 by 13 and 16 by 11 mm.

In addition to the roots which belong to the fern itself, numerous " foreign " roots are visible in the sections. In particular they are concentrated in an irregular but continuous thin belt of sclerenchyma outside, concentric with and close to the steles and meristeles. They make this belt of tissue very conspicuous while often obscuring its detailed structure. They are also abundant in the sclerenchyma of the pith adjacent to the leaf gaps (Pl. 5, fig. 8; Pl. 7, fig. 10; Pl. 8, fig. 11; Pl. 10, fig. 13). Some of these roots may be monocotyledonous, others dicotyledonous, as they show radially arranged small xylem cells containing large scattered vessels. I am indebted to Dr. Holttum for these suggestions. The roots sometimes take the place of the stelar tissues of the fern roots within a dense belt of surrounding sclerenchyma.

Structure of individual stems. The stems are clearly solenostelic. Some sections show a complete cylinder with no leaf gap (Pl. 8, fig. 11), others show a single leaf gap (Pl. 7, fig. 10; Pl. 9, fig. 12). Yet others have two leaf gaps (Pl. 5, fig. 8; Pl. 6, fig. 9). The pattern due to the development of the leaves is repeated at regular intervals in the individual stems so that the sections made at different levels across the false " stem " show successive changes. In any single section the included stems are commonly at different stages in development. Intermediate stages have been seen on the polished surfaces exposed both before and after section cutting but being unsuitable for photography they are not represented in the plates.

The periphery of the stems, inside an ill-preserved epidermis from which the ramentae arise, is formed of several layers of opaque sclerenchymatous cells with dark contents. Up to a dozen layers have been counted. Exactly similar outer tissues are described by Read & Brown (1937 : 110) in *Tempskya grandis* as the " outer cortex ". Within is a layer of sclerenchyma, at least twenty cells thick, cells which although thick-walled retain a considerable lumen. It clearly corresponds with the " middle or sclerenchymatous cortex " in *T. grandis*. Individual cells are isodiametric in cross section where the walls appear to be unevenly patchily thickened. Inside again occurs a thick layer, twenty or more cells thick, of thin-walled parenchyma (corresponding to the " inner cortex " of *T. grandis*). It is at least as broad as and may be broader than the middle sclerenchymatous cortex. Almost invariably the individual cells show black rounded objects occupying much of the cavity; sometimes these objects themselves lie in a rounded cavity within the cell. Under the quarter-inch lens most of them appear to be agglomerated crystals, although a few simple crystals are seen. In longitudinal sections of the cells they appear as clumps of elongate crystals with their long axes at right angles to the longer axes of the cells. Similar inclusions occur sparsely in the sclerenchyma of the middle cortex. Towards the inner margin of the parenchymatous zone there is always a continuous narrow band of sclerenchyma very irregular in thickness and therefore in outline as seen in transverse section. It may be sharply delimited from the parenchyma in which it lies by a dark line on the outer side, (Pl. 5, fig. 8; Pl. 8, fig. 11; Pl. 9, fig. 12), but less sharply from three or four layers of parenchyma cells which lie between it and the stele. These innermost parenchyma cells are rather small but display the same crystalline inclusions. They also occur abundantly in the irregular sclerenchyma belt just described, a belt seen only in *T. grandis* among the well preserved fossil species and in the less well preserved *T. superba* Arnold.

The stele is bounded both externally and internally by an endodermis and associated tissues. In places the endodermis is well defined as a single layer of equiaxial cells. Inside it, preserved only in certain places, are two or more layers of tangentially elongate thin-walled cells with clear cavities (Pl. 11, fig. 14). They probably represent pericycle and phloem but no sieve plates appear to be preserved. The xylem varies considerably in thickness from about three tracheids in depth to sixteen or twenty as a result of leaf trace formation. Along the margins of the xylem are patches of very small tracheids, some certainly showing scalariform thickening. The bulk of the xylem is composed of conspicuous large metaxylem tracheids with multiseriate thickening which causes them to appear angular in transverse section so producing a characteristic pattern. Where roots are about to arise the small elements at the margin become more numerous causing an outward bulge in the endodermis. It is probable that some of these are protoxylem but no spiral thickening appears to be preserved. A considerable amount of parenchyma, often with crystalline inclusions is scattered among the tracheids, again as in *T. grandis*. *T. rossica* and *T. wesselii* also show this feature (Andrews & Kern 1947 : 147) as does *T. superba* (Arnold 1958 : 137). Where the stele becomes thin and the bulge which initiates a leaf trace begins to form, the metaxylem tracheids follow a tangential course (Pl. 10, fig. 13). In the actual slide they then show the thickening clearly. At one leaf gap the end of the stele abutting on it shows what appear to be some spiral tracheids near the margin of the xylem.

Where the pith within the stele adjoins the endodermis there is a thin layer of parenchyma with the usual inclusions. It is continuous through the leaf gap with the fine parenchyma which bounds the stele externally. Otherwise almost the whole pith is formed of sclerenchyma with thick-walled cells, and, at the centre, with little lumen (Pl. 5, fig. 8; Pl. 7, fig. 10). The sclerenchyma is also continuous through the gap with the sclerenchyma of the cortical zone of the rhizome.

Scales or Ramentae. These may be very broad. One which could be measured is at least 10 mm. wide. The elongate cells which form them lie end to end and side to side. In the rows of cells the end walls are transverse or oblique to the length. The cell rows diverge towards the lateral margins of the scales where the free ends of the rows separate and form the characteristic fringed edge. Seen in transverse section of the stems they appear as thin multicellular plates of tissue (Pl. 2, fig. 5; Pl. 7, fig. 10).

Development of leaf traces and structure of meristele. On that side of the stele towards the circumference of the " false stem ", leaf gaps arise at short longitudinal intervals indicating that the leaves must have been crowded. In a single section across one stem two and sometimes three leaf-traces may still be included within the cortex and epidermis showing that they arise at acute angles (Pl. 3, fig. 6, stem *b*; Pl. 9, fig. 12). Once they have emerged from the stem they apparently change their direction and pass out of the " false stem " quickly. An occasional projecting leaf base on the side of the upright " false stem " (Pl. 1, fig. 2) points to the fact that they were borne at intervals along its length. A terminal crown may also have occurred (Pl. 2, fig. 4). The appearance of the stele in transverse section varies with the degree of development of the leaf trace, the positions of the leaf gaps and meristeles in successive sections suggesting that they were borne in two somewhat irregular rows. The stages in trace formation have been pieced together from the various stems in thin sections and cut surfaces. Serial sections were not attempted because there is only one specimen and its preservation is so patchy. This caused the sections to break irregularly and made complete transverse slices difficult to obtain. It also limited the amount of thinning that could be carried out.

Development of a trace is heralded first by the thinning of part of the stele connected with its formation while simultaneously an adjacent protuberance occurs (Pl. 6, fig. 9, rhizome *a*; Pl. 7, fig. 10). The bulge or protuberance then develops a pair of angular thickenings on the inside of the stele near its inner limits (Pl. 3, fig. 6, rhizome *b*). Further thinning at the inner ends of the bulge just beyond the thickened angles now produces a gap, first on one side and then on the other (Pl. 7, fig. 10). As a result a C-shaped trace opening inwards is separated from the stele (Pl. 9, fig. 12; cf. Pl. 6, fig. 9, rhizome *a* with Pl. 7, fig. 10). The trace passes upwards and outwards through the cortex. The angles on the inner side of the stele soon become elongated tangentially and approach one another fusing as they pass up the stem with resulting restoration of the complete cylinder.

At certain stages of development two gaps are seen in a single transverse section. In this case a semicircular section of the stele with its flattened surface towards the periphery of the " false stem " gives rise to thin outward curving lobes at its angles. The lobes separate first from the central area remaining attached at their inner ends and so producing a double convex curve on each side, the curve of the developing trace being much shorter than that of the parent stele. The central fragment of stele which may be simple or bilobed then appears as an island separated from the main stele by two developing leaf gaps (Pl. 5, fig. 8; Pl. 6, fig. 9, stem *b*). Usually one trace becomes detached as on the right in Pl. 6, fig. 9, while the other still remains attached although much thinned and ready for almost simultaneous separation.

Recently emerged leaf traces soon form elongate bulges on the stem surface even prior to their complete departure from it (Pl. 5, fig. 8, cf. *m* in Pl. 7, fig. 10 and in Pl. 9, fig. 12). The final separation of the trace as it passes through the cortical tissues next occurs. A tongue of sclerenchyma grows inward between stem and trace, one side giving off a branch which enters the bay of the meristele. Sclerenchyma from the opposite side also extends inwards until the two sides meet thereby completely surrounding both stem and leaf base (*m* in Pl. 7, fig. 10). At a slightly higher level the outermost stem tissues grow in also and divide sclerenchyma of stem and leaf base so that they completely part company (*p* in Pl. 7, fig. 10) the trace continuing upwards and outwards until it emerges at the surface of the " false stem ".

In shape the meristele becomes markedly incurved as it passes out of the stem (contrast the three meristeles in Pl. 9, fig. 12) while simultaneously its ends thicken. As is to be expected, the succession of tissues is as in the stem itself. The meristele may be only one or two tracheids thick at the middle of the arc but there are up to about seven at the incurved ends. Endodermis and associated tissues completely surround it. Owing to the angle at which traces arise transverse sections cut them somewhat obliquely so that the tissues appear blurred. The thin parenchyma which completely encircles the stele of the leaf trace and its irregular sclerenchyma is continuous with the parenchyma of the stem until separated by the ingrowing of the sclerenchyma. As in the stem the cells of this tissue show the characteristic crystalline inclusions.

An unexplained peculiarity is seen in the meristele of one thin section. Some of the tissues, more especially the parenchyma cells, have broken down and in their place oval opaque black bodies can be seen. Similar structures in a root of *Tempskya knowltoni* from Montana are described and figured by Seward (1924 : 494, pl. 17, fig. 24). He was unable to explain them but suggested that they might be coprolites of a small insect or possibly escaped cell contents. Certainly in the Kent specimen each such body occupies a separate cell until the surrounding cell walls have actually broken down. Seward adds that entomologists he consulted were unable to identify the bodies with the activities of any known boring animal and no trace of any insect had been found. " They consist ", he stated, " of finely comminuted plant debris or dark masses of rounded cell contents and are certainly not spores ".

The roots (Pl. 2, fig. 5). These vary greatly in size and are branched repeatedly. Some are as much as 2 mm. broad. Many roots and their branches grow upward through the tissues. They show a small stele with typical diarch arrangement, a well-defined endodermis surrounding it. There are about four to six large metaxylem tracheids, flanked at opposite poles by groups of about three to six small protoxylem tracheids. The metaxylem tracheids may be 0·027 mm. or less in diameter. Phloem is rarely preserved. Outside the endodermis are several layers of concentrically arranged sclerenchymatous cells with well developed cavities. They are succeeded further out by a thick band of dense sclerenchyma with cavities obliterated. In transverse section these cells appear both radially and concentrically aligned forming a very conspicuous band of tissue which may be 0·3 mm. broad. It corresponds to the " middle cortex " of Andrews & Kern in their description of *Tempskya* (1947 : 139). In young roots the sclerenchyma may be less dense. Sometimes outside the sclerenchyma there is another concentric belt of thin-walled cells of about the same width (Andrews' " outer cortex "). It is not invariably preserved. In Pl. 2, fig. 5, the " outer cortex " has a lozenge or diamond-shaped outline of which half only is preserved. This shape is dictated by the pressure of closely compacted masses of roots in the spaces between the stems. In some roots only the sclerotic tissue survives surrounding an empty circular space, occasionally occupied by foreign tissues as described above.

Affinities. The composite character of this " false stem " with its dichotomous solenostelic true stems embedded in a mass of their own roots and scales connects the specimen with the Mesozoic *Tempskya* of Corda (1845 : 81). Kidston & Gwynne-Vaughan (1911 : 13) later published a generic diagnosis of the genus quoted by Read & Brown (1937 : 108). Unfortunately the true relationship to living ferns has not yet been discovered although many distinguished botanists have carried out research on the subject. As long ago as 1872 Feistmantel suggested that *Tempskya* was not a genus but a mode of preservation of several distinct types of fern stems. To the writer, this view appears to be greatly strengthened by the occurrence of a supposed Mesozoic genus in the Tertiary. Read & Brown (1937 : 120) discuss the taxomic affinities and summarize views published prior to their paper. They created the " family " Tempskyaceae as the natural affinities could not be discovered but probably no such family exists. It is merely a convenient way of grouping different ferns with a similar habit. Dr. R. E. Holttum and Dr. T. G. Walker have kindly examined slides or detailed photographs of the Kent fern but were unable to recognize any living genus with which there is complete agreement. It is necessary to remember that the appearance of these plants in life may have differed materially from that when fossilized thanks to the cementing and hardening effects of silicification welding stems and roots into an apparently solid entity. Like Feistmantel, Andrews & Kern (1947 : 143) consider that the " trunk " of the genus " represents a peak of structural evolution that is manifest in a generally comparable fashion in a number of ferns, both living and fossil ". They refer to scattered references in literature, not quoted in detail, to living ferns having an upright trunk composed of branching stems " held together to a greater or lesser degree by a mass of adventitious roots ". Among these are, of course, some of the well-known tree ferns with a similar upright trunk or caudex which differ in important respects from *Tempskya* and all of which are certainly much larger than the Kent specimen. Writing later Andrews (1961 : 116) after briefly describing the genus commented that the radial development suggests a single stem in the early sporeling stage which grew and divided to form a large and longer trunk. He did not then consider the anatomy of the stem sufficiently distinctive to afford evidence of affinity but again emphasized that the mode of growth could have arisen independently in several unrelated groups. None known to him agreed closely with *Tempskya* either in detailed anatomy or in the huge number of stems involved. The smaller size of the Kent " false stem " with its fewer true stems strongly suggests that this specimen may eventually be matched among living material when sufficient knowledge of the anatomy and cytology of this vast group of plants is available and allowance is made for the profound alteration in appearance due to silicification. Whatever the relationship of the Mesozoic species may be it is most likely that the Kent specimen belongs to a living genus. Naturally Recent root stocks and stem bases are not available in unlimited amount or variety. The majority of *Tempskya* species are from America which has produced at least seven distinct kinds. Some of these are enormous attaining to 16 in. in diameter and a height of at least 12 or possibly 19 or 20 feet. Some include a very large number of stems. Thus Andrews & Kern (1947 : 155) quote more than 200 stems in a single trunk. Some of the American species are well preserved and fall into two clear groups (Read & Brown 1937 : 119; Andrews & Kern 1947 : 147). The Kent " stem " closely agrees in its detailed morphology with *T. grandis* Read & Brown (1937 : 114, pl. 29, fig. 2; pl. 32, figs. 2–5; pl. 33, figs. 1–4; pl. 34, figs. 1–4; pl. 35, figs. 1–4; pl. 41, fig. 4; pl. 42, figs. 1–3; pl. 43, figs. 1, 4–7) which belongs to the first of these groups. It is an Upper Cretaceous species from the Aspen shales of Wyoming. It is about 8 cm. in diameter and some 20 cm. long, perhaps larger because more mature than the Kent fossil. Despite its somewhat worn appearance, so that one or two of its stems are abraded longitudinally on the outer side, it looks as if the whole " trunk " approximated closely to the original dimensions for the reasons given on p. 172. The increased abundance of roots near the base and the failure of preservation of other detail in the basal part suggests that this is near to the true base of the specimen which, must, therefore, have been on a much smaller scale than other known species.

Summarizing points of resemblance, some of which have been mentioned in the description, the Kent *Tempskya* and *T. grandis* have in common: xylem containing an appreciable amount of parenchyma; an inner parenchymatous cortex which encloses a constant but narrow irregular band of sclerenchyma close to but not contiguous with the stele; a similar narrow zone of parenchyma forming the outer layers of pith in contiguity with the stele and with the sclerenchyma inside; large individual stems in the false " stem " with rather short internodes. Thus apart from difference of size which may not necessarily be of great significance the material of the Kent specimen can only be distinguished from *Tempskya grandis* by the smaller number of meristeles in the transverse sections of the rhizomes. It has from one to three, commonly two meristeles, whereas in *T. grandis* there are two to five, commonly three or four, implying greater crowding of the leaves in this latter species (cf. Read & Brown 1937 : 115, text-fig. 3, pl. 28, fig. 2 [Note the erratum slip]; pl. 32, figs. 2–5; pl. 33, figs. 1–4).

T. superba described by Arnold (1958 : 138) has suffered obliteration of much detail by complete silicification of the tissues. Form and size of individual stems are retained and there is enough structure to show a strong resemblance to *T. grandis* in that both have the distinctive continuous but irregular sclerotic layer in the inner cortex absent in other species except the Kent form. All three also have sclerenchyma in the pith. Arnold separates *T. superba* from *T. grandis* partly on the much larger size of its stems which he gives as at least 1 cm. in diameter without attached leaf bases, 2 cm. if they be included. He infers that the diameter of *T. grandis* (stems) is 6–7 mm. but according to measurements based on Read & Brown's figures the two species appear to approach one another in this respect, while in the Kent *Tempskya* a considerable range of size occurs in the one specimen depending on the position within the length of the stem (cf. p. 172). Size of stem alone, therefore, does not appear to be a sufficient reason for separation. The holotype of *T. grandis* is 8 cm. in diameter, 20 cm. long. That of *T. superba* was a slab measuring about 6 by 12 cm., 2 cm. thick before cutting. It was obviously very incomplete. Both greatly exceed the dimensions given for the Kent specimen (see p. 172). *T. superba* normally shows four or five foliar traces (meristeles) in each stem section, indicating, as in *T. grandis* exceptionally short internodes. On the grounds of number of foliar traces it therefore appears that the *Tempskya* from Kent is distinct from these two species which otherwise it closely resembles in detailed cytology. *T. superba* was found in an eroded Oligocene deposit in Nebraska but is believed to have been derived from the Lower Cretaceous Dakota Sandstone.

As only one specimen from Kent is in existence it is merely described as *Tempskya* sp. It is the second species to have been discovered in England. A much earlier record is *T. erosa* Stokes, Webb & Mantell from the Wealden Beds or Lower Greensand of Tilgate Forest, Hastings and Potton. *T. erosa* differs completely in its character and preservation from *Tempskya* sp. described here. Its numerous much smaller stems show little structure in detail but are embedded in dense masses of innumerable roots. It has been re-described and discussed by Stopes (1915 : 16) and more recently illustrated by Seward (1924, pl. 16, fig. 4; pl. 17, fig. 16). It is so different in every way that it does not concern us here any further.

Origin of the Specimen. As soon as the specimen was referred to *Tempskya* it raised the question whether a supposed Mesozoic form found at Sheppey could have come from the London Clay, especially in view of the silicious preservation (see p. 171). Mr. G. F. Elliot has pointed out that a similar preservation is known in Palm and dicotyledonous wood, in *Osmunda dowkeri* and in cones of *Pinus macrocephalus* from Herne Bay. *Pinus macrocephalus* is occasionally picked up on the shore between Bishopstone and Reculvers where the Thanetian outcrop is exposed. Some of the above have been attributed to the Thanet Sands, others to the London Clay but their preservation is different from that of *Tempskya* except in the case of the dicotyledonous woods from Herne Bay. A few of these (B.M.N.H., V.27923) which have closely comparable and characteristic preservation have come from unweathered foreshore outcrops of the Woolwich Bottom Bed in Herne Bay. Material washed out of the Thanet Sands has been found well to the west of Herne Bay hence *Tempskya* could have been transported naturally to the beach at Sheppey. To summarize, the preservation suggests that the Lower part of the Woolwich Beds at Herne Bay is the most likely source of the specimen. The difficulty of accepting such a source is eliminated if, as seems probable, such a habit of growth is not confined to the Mesozoic

The photographs were taken in the Photographic Department of the British Museum (Natural History). The typing was done by Mrs. M. Firth. To all the persons concerned and to those already mentioned in the text the author's warmest thanks are given.

REFERENCES

Andrews, H. N. 1961. *Studies in Paleobotany.* xii + 487 pp. New York.

Andrews, H. N. & Kern, E. M. 1947. The Idaho *Tempskya* and Associated Fossil Plants. *Ann. Mo. bot. Gdn.*, **34** : 119–186, pls. 15–27.

Arnold, C. A. 1958. A new *Tempskya. Contr. Mus. Paleont. Univ. Mich.*, **14** : 133–142, 3 pls.

Corda, A. J. 1845. *Flora protogaea: Beitrage zur Flora der Vorwelt.* 128 pp., 50 pls. Prague.

Feistmantel, O. 1872. Über Baumfarrenreste der böhmischen Steinkohlen, Perm - und Kreide-formation. *K. böhm. Gesell. Wiss. Abh.*, **6** : 1–30, pls. 1, 2.

Kidston, R. & Gwynne–Vaughan, D. T. 1911. On a new species of *Tempskya* from Russia. *Russ. K. min. Gesell. Verh.*, **48** : 1–20, pls. 1–3.

Read, C. B. & Brown, R. W. 1937. American Cretaceous Ferns of the genus *Tempskya. Prof. Pap. U.S. geol. Surv.*, **186** : 105–131, pls. 28–43.

Seward, A. C. 1924. On a new species of *Tempskya* from Montana: *Tempskya Knowltoni* sp. nov. *Ann. Bot.*, **38** : 485–507, pls. 16, 17.

Stopes, M. C. 1915. *Catalogue of the Mesozoic Plants in the British Museum (Natural History). The Cretaceous Flora. Part II. Lower Greensand (Aptian) Plants of Britain.* xxxvi + 360 pp. 32 pls.

DESCRIPTION OF PLATES

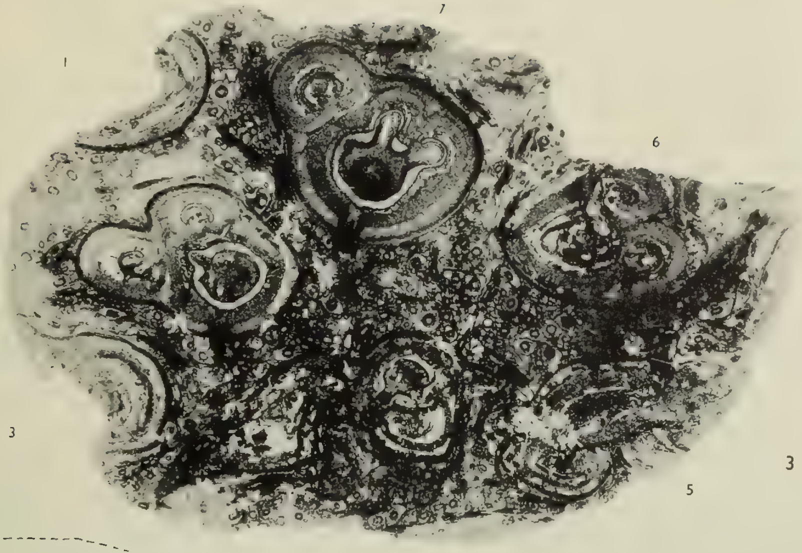
Note. The photographer has taken Pl. 1, fig. 3 and Pls. 3–5 from the back of the slide. Allowance must be made for this mirror image when examining the plates in order to study the development of the stele and leaf traces in the rhizomes.

PLATE 1

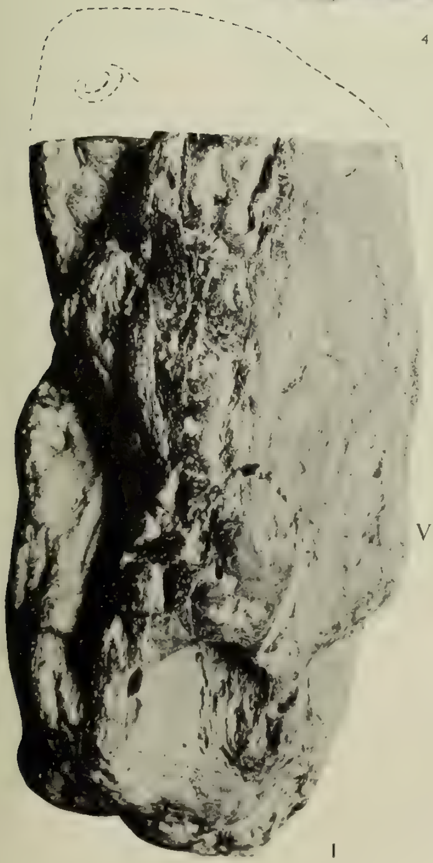
***Tempskya* sp.**

FIGS. 1, 2. " False stem " from opposite sides. The apex has been removed. V.51841, upper surface of fragment so numbered. Position of slides is at *f*, *g–i*. On the left in Fig. 1 dichotomous forking of the small stems is seen. The white hollow at base shows scales in the actual specimen and upwardly directed roots. In Fig. 2 rounded projections at *p*. are much abraded petiole bases. × 1 approx.

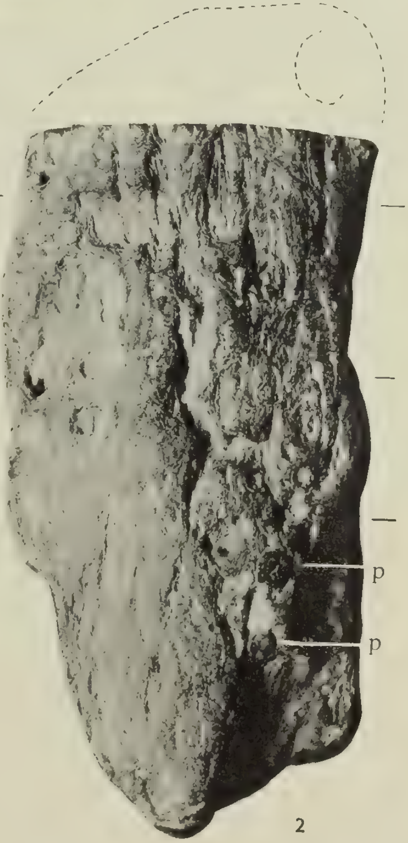
FIG. 3. Transverse section of " stem" somewhat crushed and disorganized in the lower half. Seven numbered true stems are visible (part only preserved of 1 and 3), 2 and 7 are embedded in roots and scales of " stem " so do not in this section touch the surface of the specimen. 4 is in process of dichotomous division, 5 and 6 are rather poorly preserved. × 2. V.51841*f*.



3



1


g – i
f
V.51841
p
p

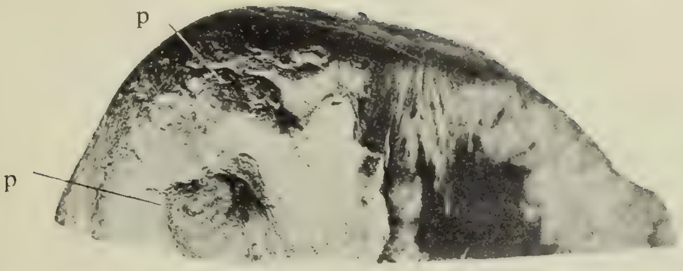
2

PLATE 2

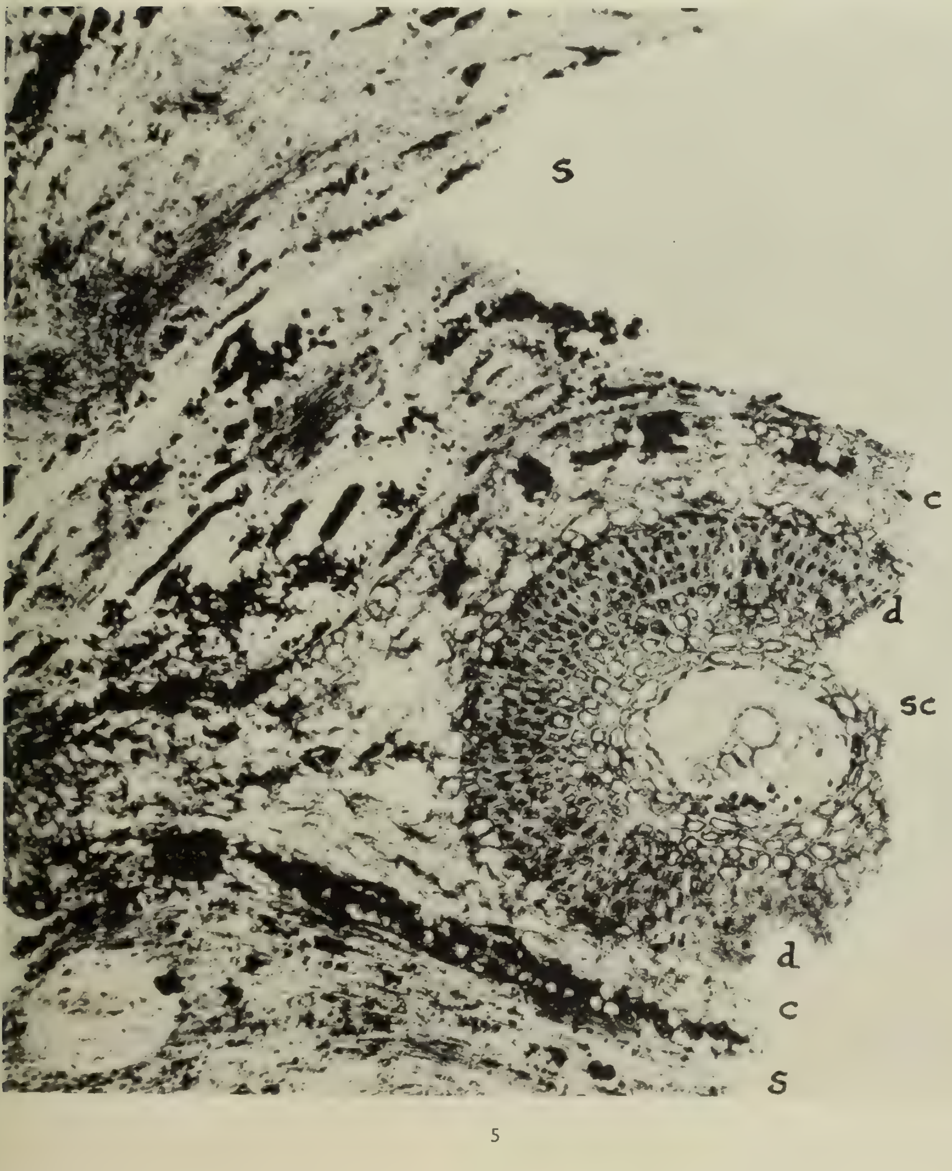
Tempskya sp.

FIG. 4. Side of severed apical fragment showing projecting petioles at *p*. Fragment cut longitudinally on right in preparing other sections but here shows only roots and scales out of focus. ×2. V.51841*b*.

FIG. 5. Transverse section of typical diarch root penetrating scales arising from the epidermis of a stem. Large metaxylem tracheids occupy centre of root and are flanked by two patches, at opposite poles, of small protoxylem tracheids. Tissues outside xylem, including endodermal ring, decayed (white in figure). Next come three concentric and radial rows of sclerenchyma, *sc*, with cavities. Outside again are four to five rows of dense sclerenchyma cells, *d*, with blocked cavities. A diamond-shaped area (left half only preserved) of thin-walled cells beyond the sclerenchyma is cortex, *c*. The multicellular character of scales, *s*, can be seen obscurely (out of focus). ×*ca* 90. V.51841*i*.



4

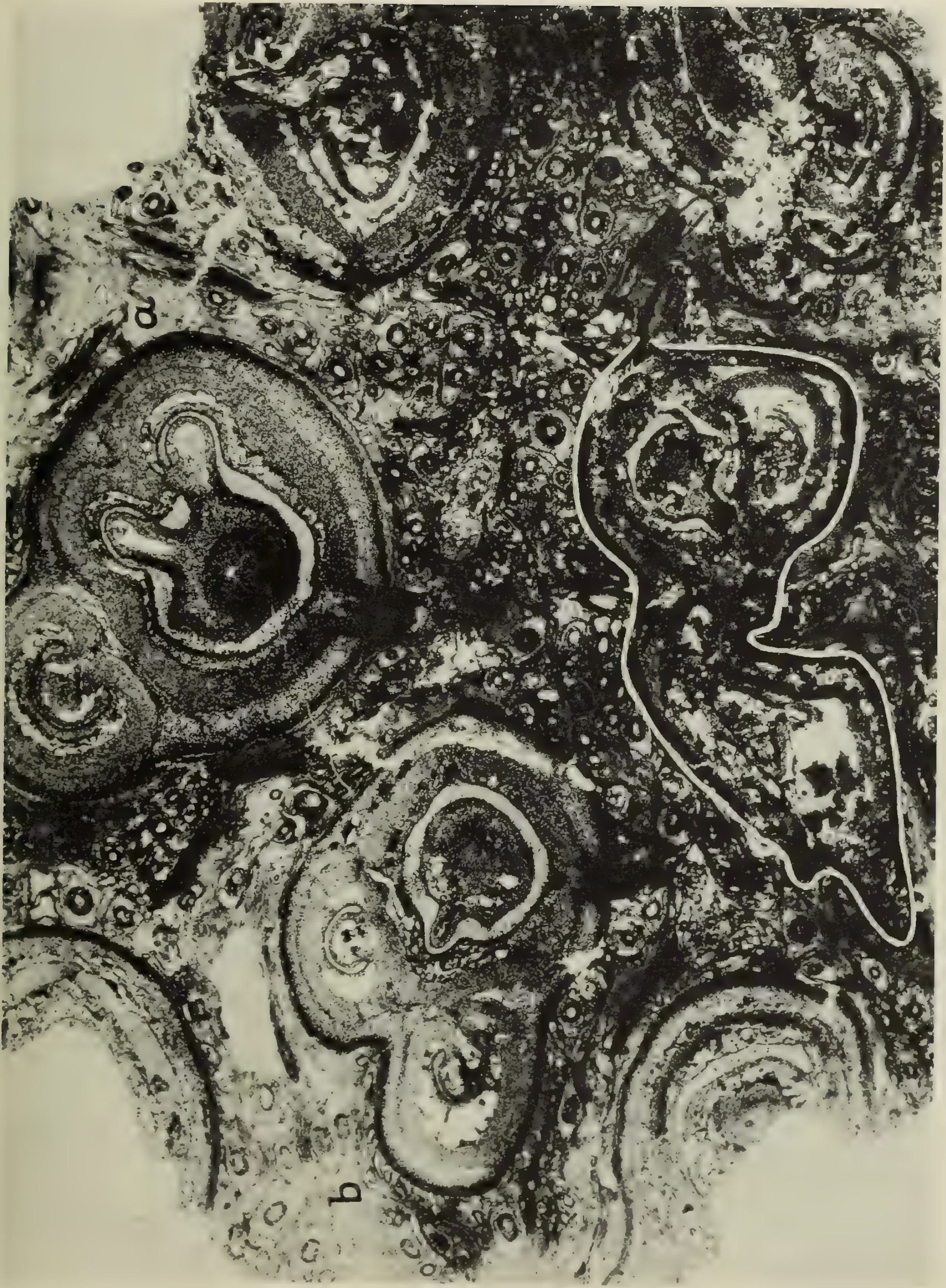


5

PLATE 3

Tempskya sp.

Fig. 6. Part of slide V.51841*f* shown in Plate 1, fig. 3. The mass of roots and scales in which the stems are embedded are sectioned in various directions. Stem *b* (2 in Pl. 1, fig. 3) shows a typical cylindrical stele with protuberance on the left marking initiation of a leaf trace. Detached meristeles of two incipient leaf-bases are also seen. Stem *a*, (7 in Pl. 1, fig. 3) shows a stele with two leaf gaps one each side of a small island of xylem. Two curved arms of stele indicate leaf traces not yet severed. A stem at *c* (4 in Pl. 1, fig. 3) which has begun to divide dichotomously is, in consequence, bilobed. It is outlined in white but is shown untouched and more highly magnified in Pl. 4, fig. 7. The obscure appearance is caused by the partial decay and dislocation on this side of the " stem " but the two new steles are already separated. × 5·5.

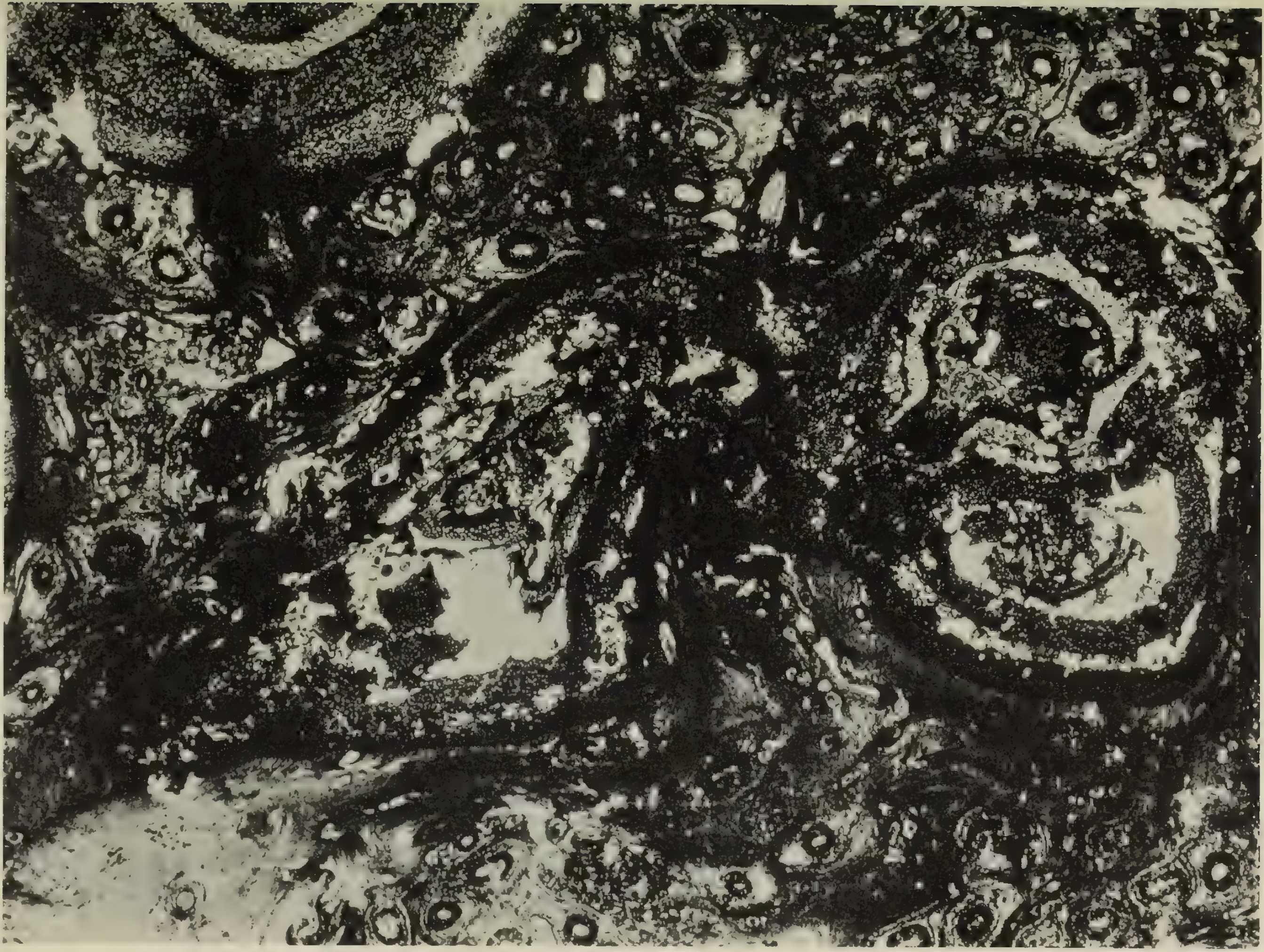


6

PLATE 4

Tempskya sp.

FIG. 7. The dividing stem in Pl. 3, fig. 6 (the right margin of the figure just cuts the edge of the stem). Originally a cylinder the stele on the right has been crushed and consequently dislocated in four places. One break passes through the prominence on the left which indicates the beginnings of a leaf trace. A meristele which has already separated is seen (surrounded by white) below the stele. The second stele in the left lobe of the dichotomy is also distorted but, again, the lobe (dislocated) of an incipient leaf trace is visible (above white patch). × 10. V.51841*f*.



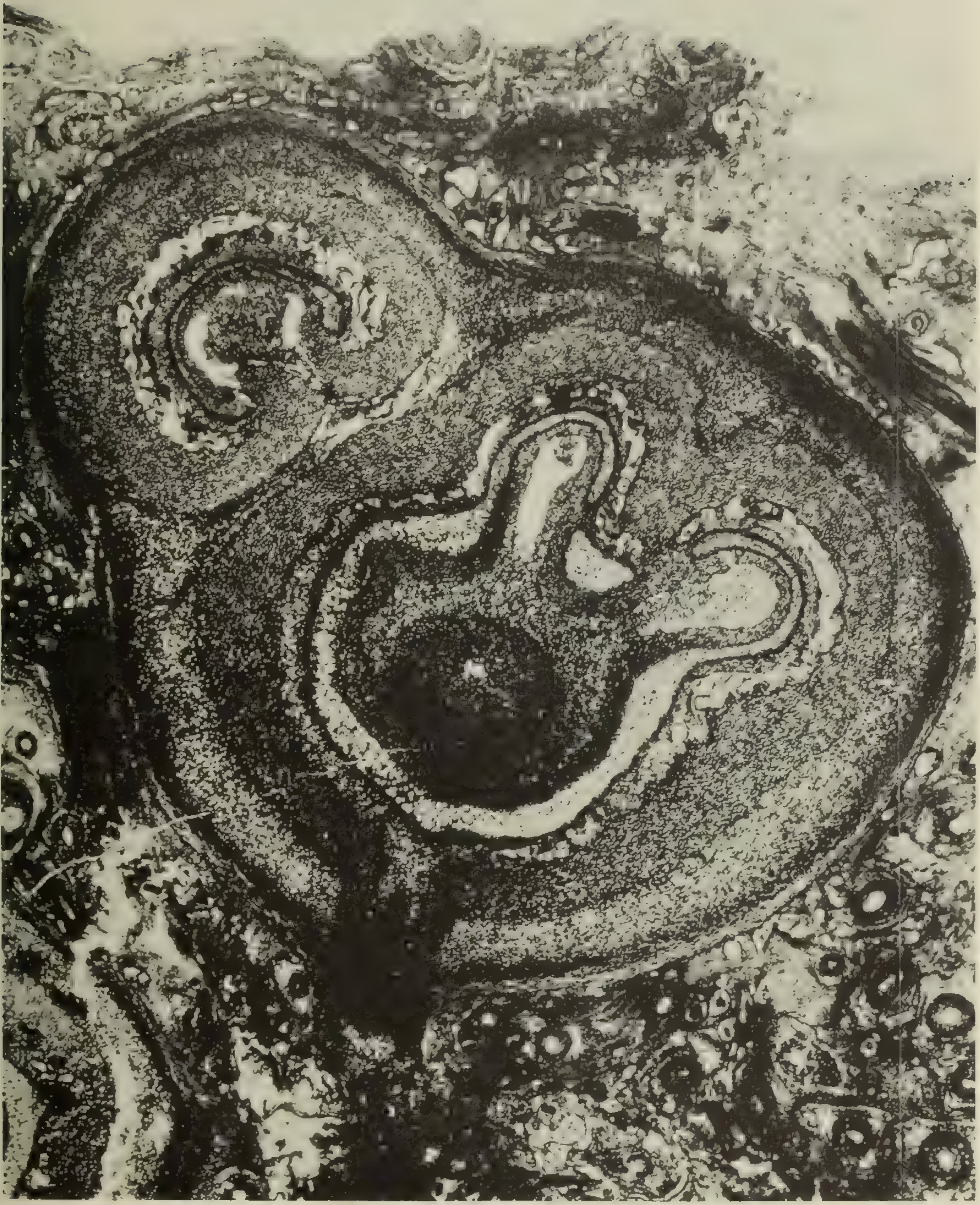
7

PLATE 5

Tempskya sp.

Fig. 8. The join on the right was due to the stem lying in part on two negatives.

Stem *a* in Plate 3, fig. 6. Dark band at base crossing cortex and epidermis is a root. The two leaf gaps flanking the island of stele are better seen here as are the curved incipient meristeles on each side. The curved loop on the left is almost separated but that on the right is still fully attached. A deeply curved leaf-trace (top left) is about to emerge. It is already partially cut off from the parent stem by ingrowing sclerenchyma from the two sides. Both parent stele and meristele are partly embraced externally by an irregular band of sclerenchyma much infested with " foreign " roots. This belt of tissue is surrounded by parenchyma on both sides. × 10. V.51841*f*.

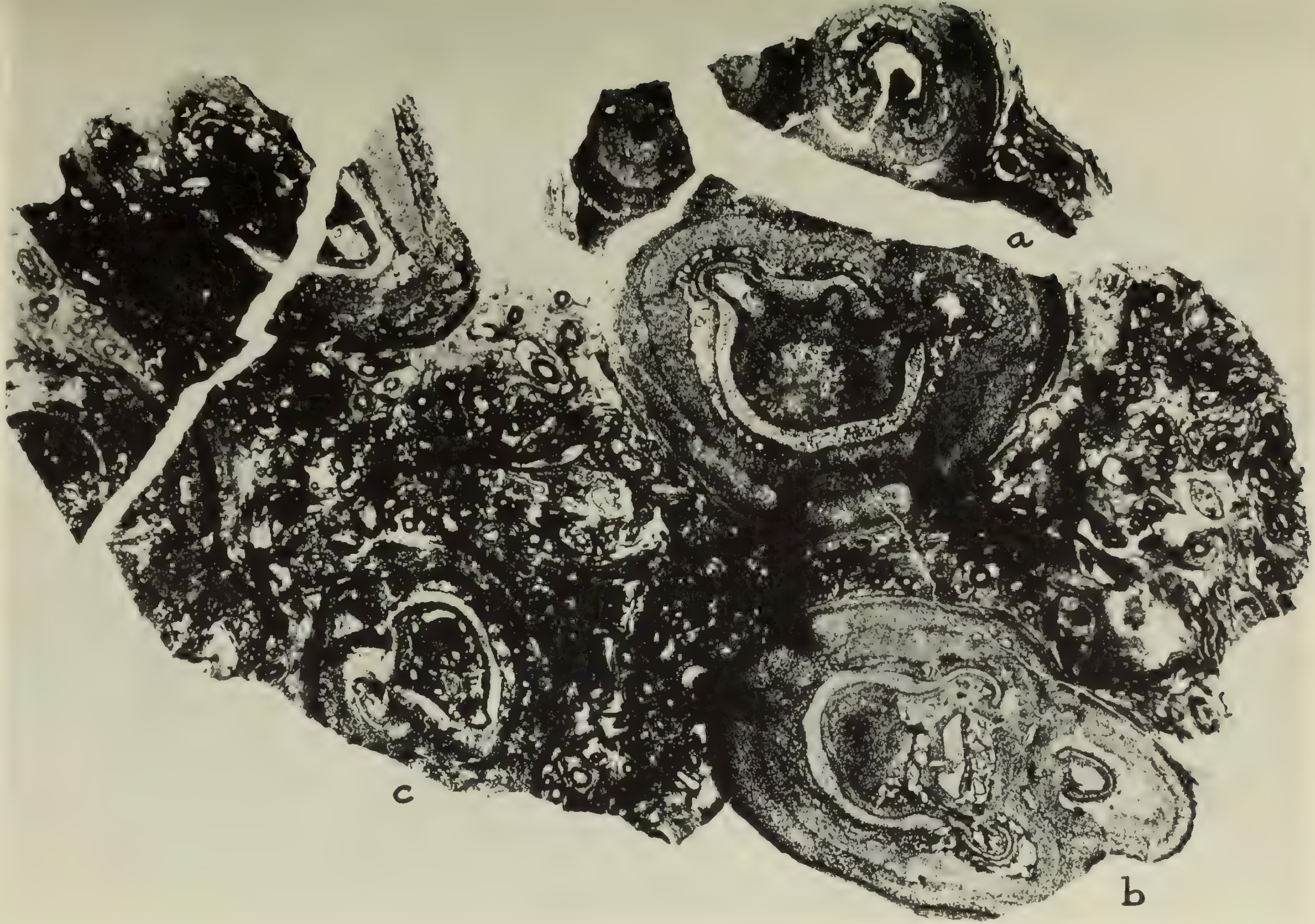


8

PLATE 6

Tempskya sp.

FIG. 9. Stems *a*, *b* and in part *c* show a later (younger) stage of these stems in Plate 3 (reversed as in a mirror). The stele bounding one leaf gap (in *a*) has now united again with the central island of xylem and forms the loop for a new meristele. The meristele on the left in Pl. 3 has separated and moved out into the cortex (right in Pl. 6). The other leaf gap still persists. In *b* the bulge seen on the left in Pl. 3 has separated from the stelar ring (on right in Pl. 6); the angular thickenings flanking the bulge in Pl. 3 have elongated and united, but two new loops have formed, one on each side of the bilobed fused xylem from which they have severed themselves at their upper ends thereby producing two curved loops and two leaf gaps. The lower limb in Pl. 6 has just separated from the stem stele. In *c* the formation of another stele is visible. ×5. V.51841*g*.

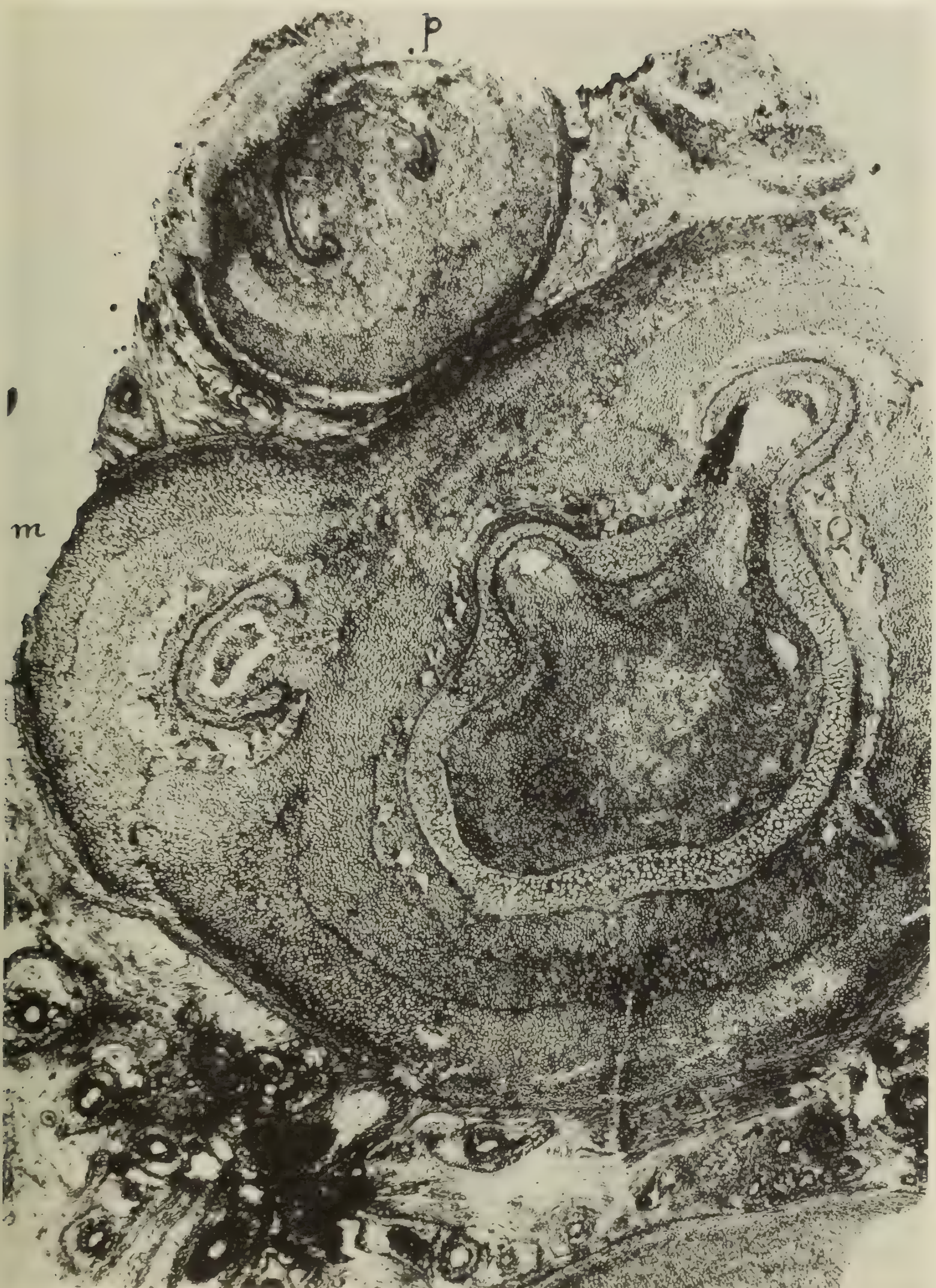


9

PLATE 7

Tempskya sp.

FIG. 10. A yet higher level in stem *a*. The loop in Pl. 6, top left, has now formed a new meristele. The gap in the stele of the stem still persists but another loop at the end of the lower free limb is about to initiate another meristele. The leaf trace (top right) is now free from the parent stem and is surrounded by its own epidermis. The successive cortical coats (see p. 173) are well marked. The irregular sclerenchyma belt within the parenchyma around the stele is little infested with " foreign " roots here, less so than in the young meristele (centre, above). The scales arising from the epidermis are well preserved but the magnification is insufficient to show the multicellular structure. × 10. V. 51841*h*.

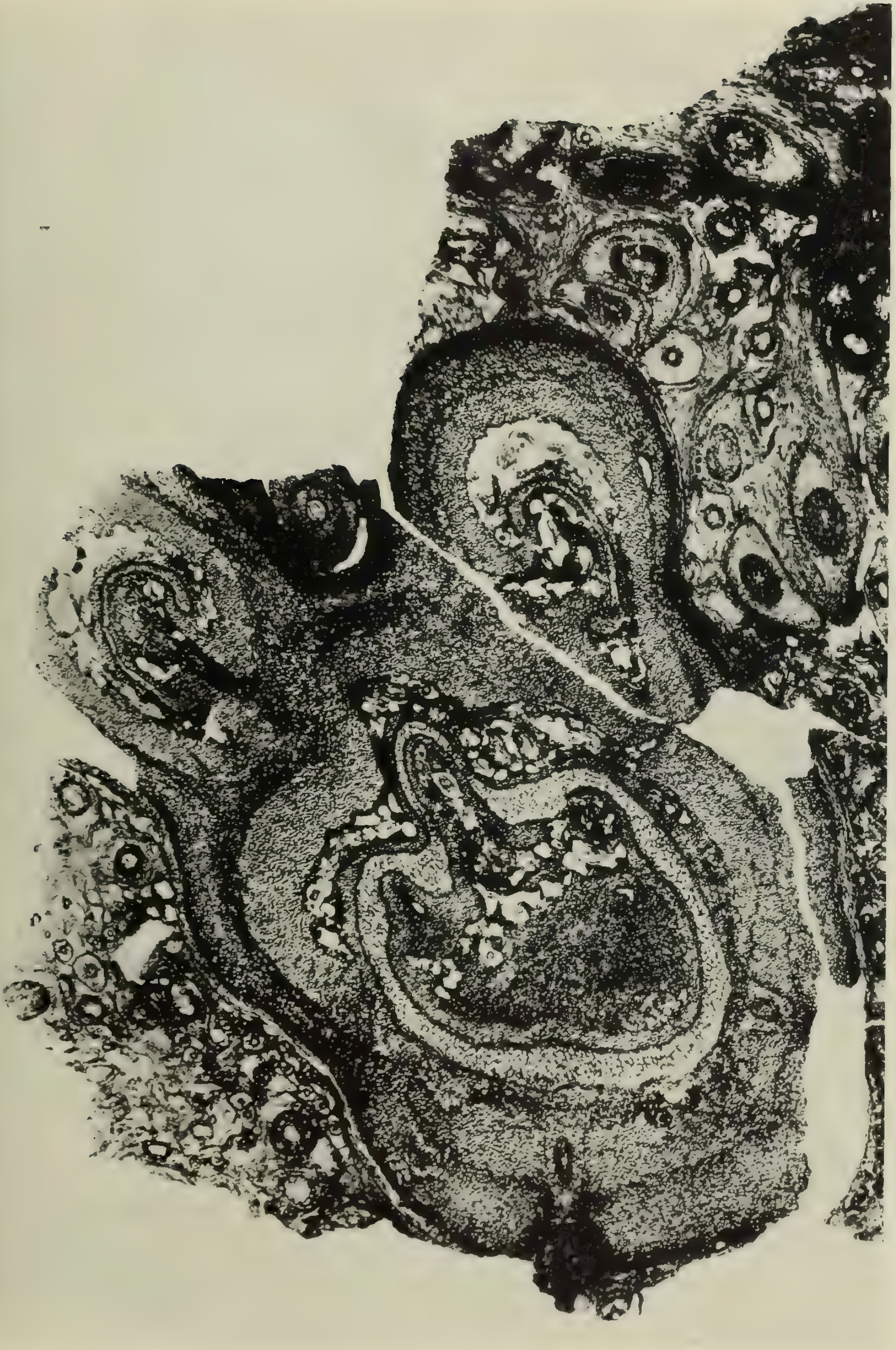


10

PLATE 8

Tempskya sp.

FIG. 11. Stem *b* at a higher level than in Pl. 6, and differently oriented. The meristele of Pl. 6 has separated from the stem and is not shown in this section. The bilobed island of stele in Pl. 6 has reunited with the arms of the main stele from which the incipient meristeles, there seen as curved extremities, have here separated and moved outwards. The upper of these two meristeles is now partly separated from the stem stele by the ingrowing of the outermost band of sclerenchyma. " Foreign " roots are clearly shown in the pith sclerenchyma and in that outside the main stele itself. The narrow loop of a new meristele is seen on the radius between the two separated meristeles. × 10. V. 51841*i*.

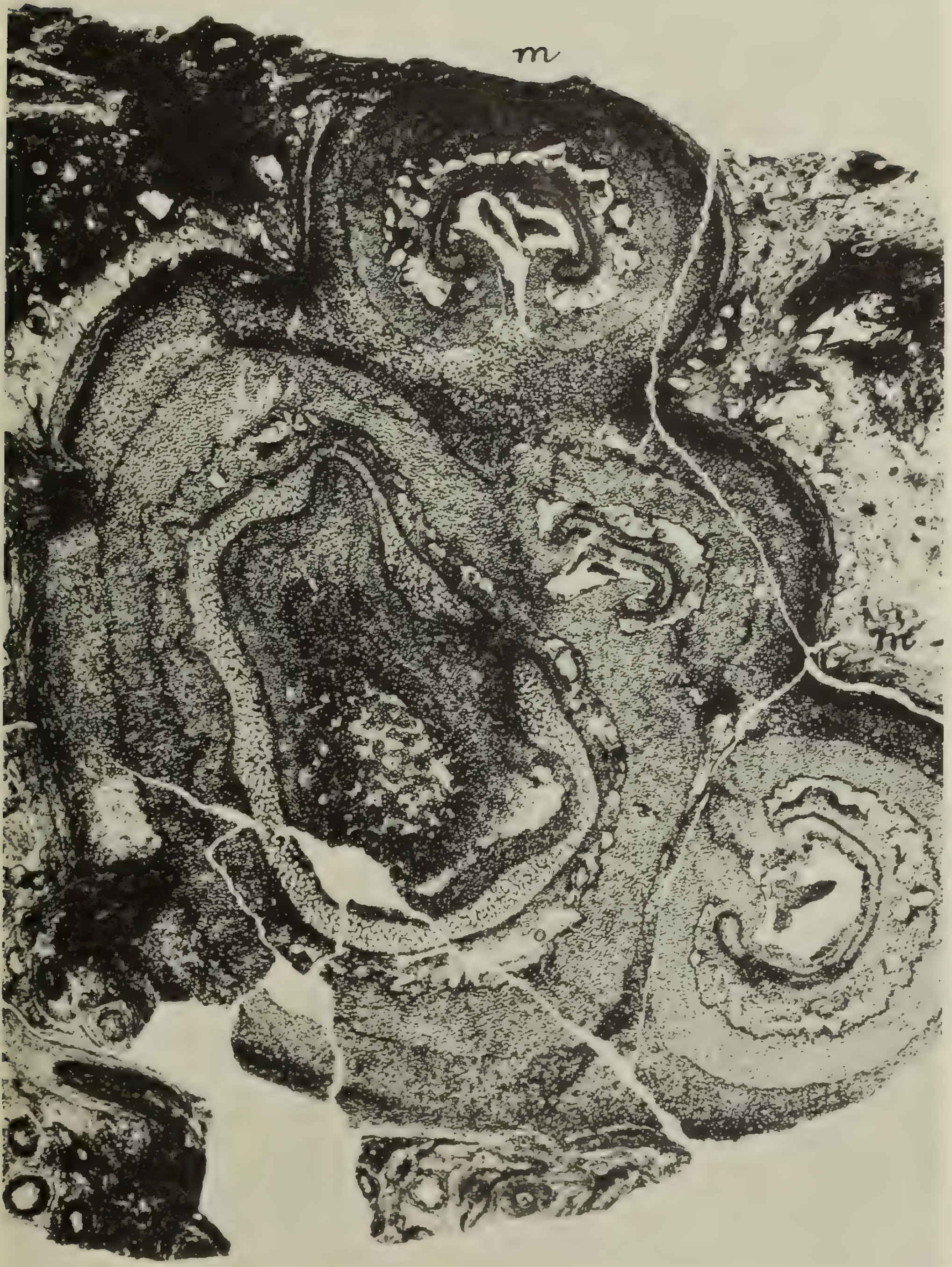


11

PLATE 9

Tempskya sp.

Fig. 12. A higher section through stem *a*. The loop in the stele in Pl. 7 has separated to form a meristele leaving a new leaf gap while the gap seen in Pl. 7 has closed. The curved hook-like free end of the stem stele in Pl. 7 has passed out as a meristele (right, below) partially separated by ingrowing sclerenchyma. The meristele above in Pl. 7 is now almost separated from the parent stem as is evident from the constriction which has formed on each side of it and the thick sclerenchyma between the two. The separated trace in Pl. 7 has grown right out of the " false stem ". The successive coats: epidermis with thin outer cortex, sclerenchymatous middle cortex, thick parenchymatous inner cortex with included irregular band of sclerenchyma just outside the stele but separated from it by parenchyma, are clearly seen. × 10. V.51841*i*.

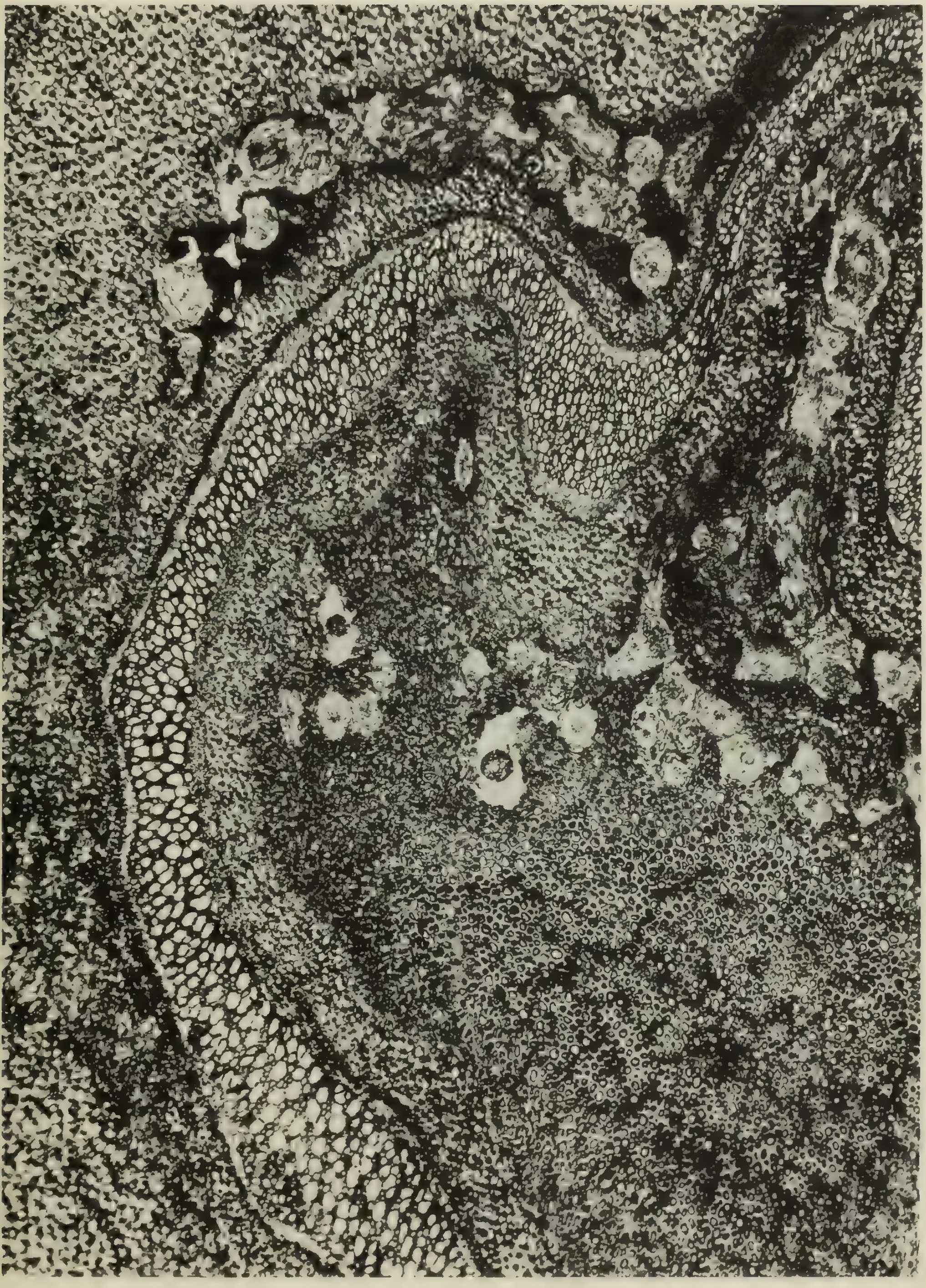


12

PLATE 10

Tempskya sp.

FIG. 13. An arc of the stele in Pl. 8. It shows the large metaxylem tracheids with scattered patches of parenchyma among them. Small tracheids are seen at the lower angle of the thickened part of the stele above which, to the right, transverse orientation of tracheids is apparent where a leaf gap is in process of development. Parenchyma cells with black crystalline inclusions are seen in the inner cortex, and these cells abut on the stele on both sides. Thick-walled sclerenchyma with small cavities shows clearly in the centre of the pith but is largely obscured by " foreign " roots in the irregular sclerenchyma belt of the inner cortex outside the stele and, in places, in the pith. ×35. V.51841*i*.

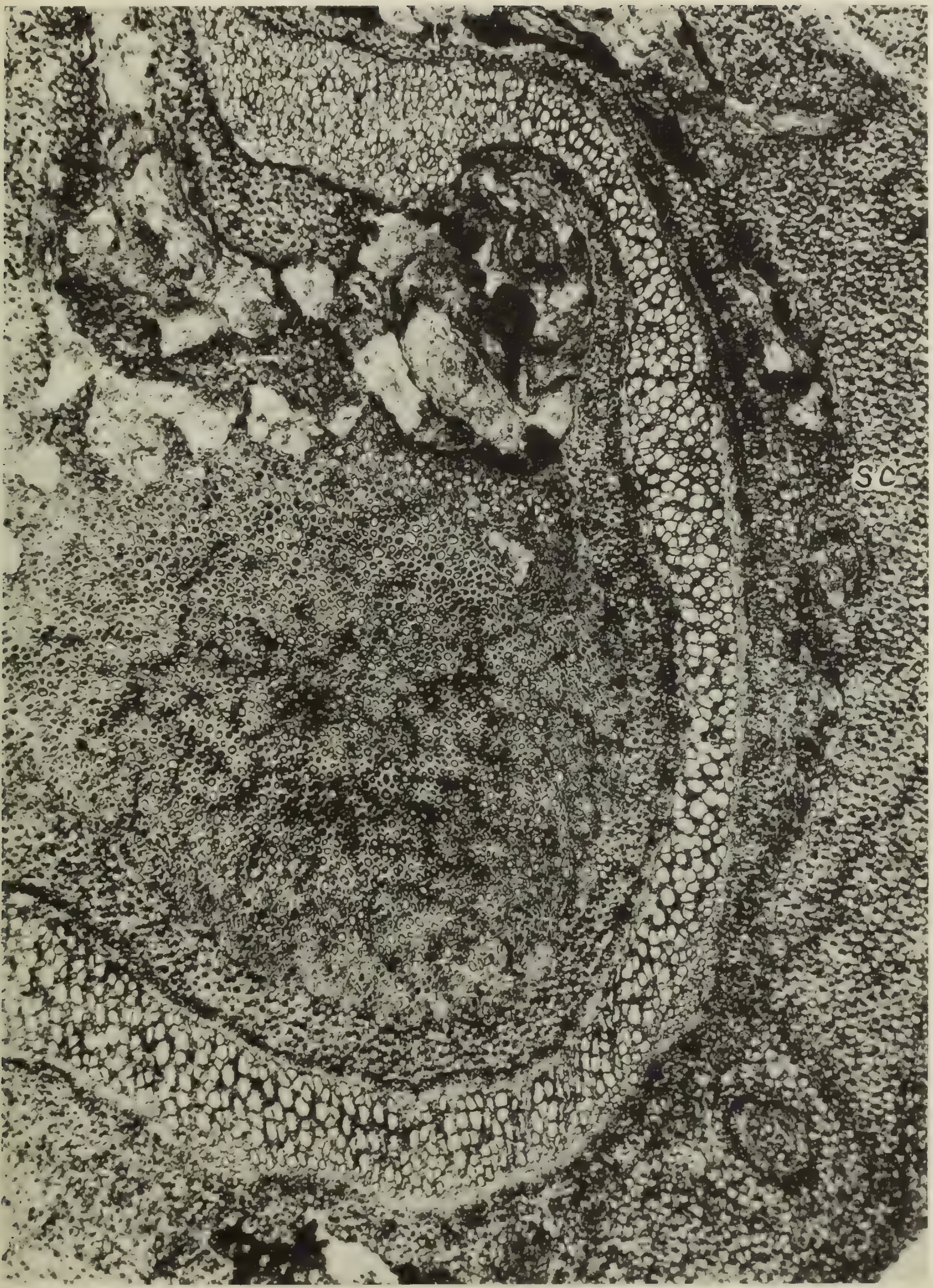


13

PLATE 11

Tempskya sp.

Fig. 14. Stelar arc on the opposite side of the stele in Pl. 8. Sclerenchyma cells of the irregular band are seen at *sc* in the parenchymatous inner cortex where " foreign " roots are absent. Small marginal tracheids are well developed in the south-east corner of the stele and especially where roots are in process of formation. Tangential cells associated with endodermis are visible on the right. Other features as in Pl. 10. ×35. V.51841*i*.

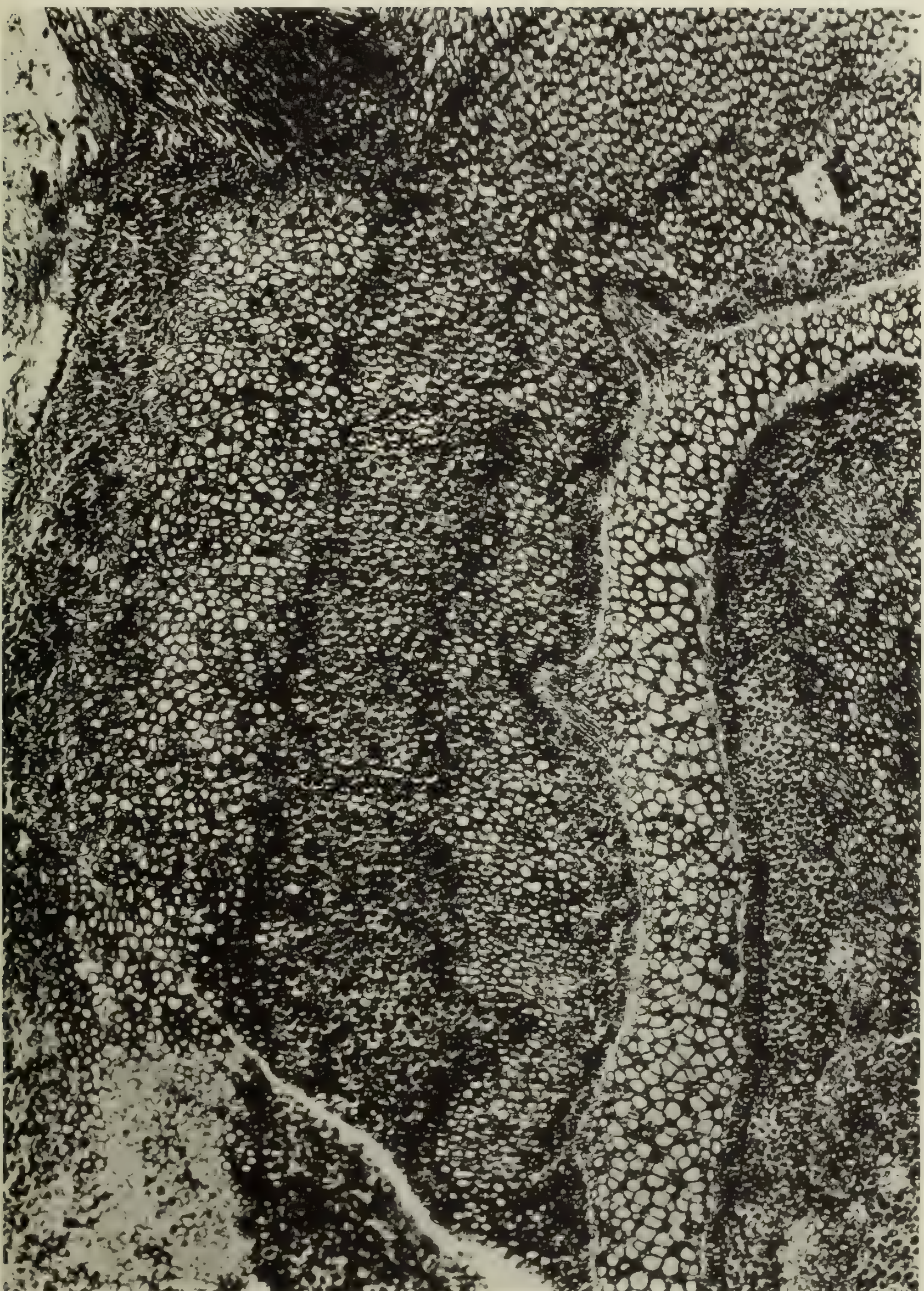


14

PLATE 12

Tempskya sp.

FIG. 15. An arc of stele in Pl. 9, stem *a*, showing the origin of two roots. Scales arise from the epidermis (top left) where also a large root emerges from the stem. Dense outer cortex is visible (top left) sharply differentiated from the sclerenchyma of the middle cortex which in its turn is distinct from the parenchyma with black crystalline inclusions of the inner cortex. The irregular sclerenchyma belt of the inner cortex lies outside the stele but separated from it by a thin layer of the parenchyma. The endodermis is somewhat blurred owing to the slight obliquity of the section but can be seen in places in the slide by focusing. Associated tangentially elongate cells are clear in the slide, obscurely seen in the figure (right, inside stele). ×35. V.51841*i*.



15

12 JAN 1968
NATURAL HISTORY

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

BRITISH MUSEUM
25 [illegible]
NATURAL HISTORY

COLONIAL PHILLIPSASTRAEIDAE FROM THE DEVONIAN OF SOUTH-EAST DEVON, ENGLAND

C. T. SCRUTTON

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 5
LONDON: 1968

COLONIAL PHILLIPSASTRAEIDAE FROM THE DEVONIAN OF SOUTH-EAST DEVON, ENGLAND

BRITISH MUSE
25 MA
NATURAL H

BY

COLIN THOMAS SCRUTTON x-ref.

Pp. 181–281; 18 *Plates*; 21 *Text-figures*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 5
LONDON: 1968

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 15, *No.* 5 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation:
Bull. Br. Mus. nat. Hist. (Geol.)

© Trustees of the British Museum (Natural History) 1968

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 19 *March,* 1968 *Price* £4

COLONIAL PHILLIPSASTRAEIDAE FROM THE DEVONIAN OF SOUTH-EAST DEVON, ENGLAND

By C. T. SCRUTTON

MS accepted April 26th 1967

CONTENTS

Page

I. INTRODUCTION 184
II. ACKNOWLEDGMENTS 184
III. STRATIGRAPHY 185
 (a) Middle Devonian 185
 (b) Upper Devonian 188
IV. GENERAL PALAEONTOLOGY OF THE COLONIAL PHILLIPSASTRAEIDAE 190
 (a) Microstructure 190
 (b) Increase. 193
 (c) Variation 198
  (i) Introduction 198
  (ii) Variation in diameters 200
  (iii) Variation in septal number and the septal ratios . 203
  (iv) Variation in size ratios 205
V. SYSTEMATIC DESCRIPTIONS 205
 Family Phillipsastraeidae C. F. Roemer 208
  Genus *Phillipsastrea* d'Orbigny 210
   P. hennahi hennahi (Lonsdale) 214
   P. hennahi ussheri subsp. nov. 221
   P. devoniensis (Edwards & Haime) 226
   P. ananas (Goldfuss) 228
   P. rozkowskae sp. nov. 230
  Genus *Frechastraea* nov. 231
   F. pentagona pentagona (Goldfuss) 233
   F. pentagona minima (Różkowska) 236
   F. micrommata (C. F. Roemer) 240
   F. carinata sp. nov. 242
   F. goldfussi (de Verneuil & Haime) 247
   F. bowerbanki (Edwards & Haime) 253
  Genus *Thamnophyllum* Penecke 257
   T. germanicum germanicum nom. nov. 260
   T. germanicum schouppei nom. nov. 261
   T. caespitosum (Goldfuss) *sensu lato* 265
   T. caespitosum paucitabulatum subsp. nov. . . . 267
   Thamnophyllum spp. 271
  Genus *Peneckiella* Soshkina 271
   P. salternensis sp. nov. 273
VI. REFERENCES 275

SYNOPSIS

The classification of the family Phillipsastraeidae Roemer is critically reviewed. Twelve species belonging to the genera *Phillipsastrea*, *Frechastraea* gen. nov., *Thamnophyllum* and *Peneckiella*, and including *Phillipsastrea hennahi ussheri* subsp. nov., *P. rozkowskae* sp. nov., *Frechastraea carinata* sp. nov., *Thamnophyllum caespitosum paucitabulatum* subsp. nov. and *Peneckiella salternensis* sp. nov. are described from the Middle and Upper Devonian of the Torquay, Paignton and Newton Abbot areas of south-east Devon. New names are proposed for *Thamnophyllum trigeminum* Penecke and *Macgeea* (*Thamnophyllum*) *minima* Schouppé. Detailed statistical studies of variation in species and subspecies samples and individual colonies of many of the taxa are described and analysed. The stratigraphy of the more important localities from which phillipsastraeids have been collected is briefly reviewed.

I. INTRODUCTION

NOT until the work of Schouppé (1958), over one hundred years after Lonsdale (1840) had erected " *Astrea hennahii* ", was the presence of horseshoe dissepiments in this, the type species of the genus *Phillipsastrea* generally accepted. An earlier record of this fact by Smith (1945 : 37), who placed very little emphasis upon it, appears to have passed without notice. Schouppé, however, considered dissepimental form and the associated trabecular structure to be of particular taxonomic importance in the group of Devonian rugose corals with which *Phillipsastrea* is associated. He thus attempted a thorough revision of their classification, but his suggestions are, in part, unacceptable where they bring together species with markedly different morphological characteristics, unlikely to have been closely related.

The type locality of " *Astrea hennahii* " is Barton Quarry, Torquay (south Devon) and many of the colonial species and genera closely related to *Phillipsastrea* are also well represented in this area. These English corals have not been examined in detail since the middle of the last century, when Edwards & Haime (1853) described them, and their taxonomic revision is long overdue.

In the present paper the classification of the phillipsastreids is critically surveyed and the colonial species and genera of the Phillipsastraeidae from south-east Devon are described. As far as the material allows, the variation in the taxa described has been investigated statistically. Data collected for individual colonies of most of the species and subspecies enable, in addition, some comparisons to be made between specific and colonial variation.

In the course of this work it has been necessary to examine a number of species formerly considered as phillipsastreids, but which are now removed from the Phillipsastraeidae. These corals all belong to the family Marisastridae and have been described elsewhere (Scrutton 1967).

The following abbreviations are used: BM(NH) British Museum (Natural History); OUM University Museum, Oxford; GSM Geological Survey Museum, London; TM Torquay Museum; TM(JB) Jukes-Browne Collection in the Torquay Museum; GVM Dr. G. V. Middleton's Collection, Murchison Museum, Imperial College, London.

II. ACKNOWLEDGMENTS

This work formed part of a thesis submitted for the degree of D.Phil. at the University of Oxford. The author is indebted to both the Trustees of the Durham Colleges Research Studentships (Durham University) and the Burdett-Coutts Research Studentships (Oxford University) for financial support.

The author is particularly grateful to Professor M. R. House (Hull) who supervised the work and to Professor Maria Różkowska (Poznàn, Poland) and to the late

Dr. H. Dighton Thomas (British Museum (Nat. Hist.)), for invaluable discussion on all aspects of this paper. Acknowledgment is due to the curators of the Museums mentioned in the text, all of whom have been most helpful in making available specimens in their care. The photographs were taken by Mr. Peter Green at the British Museum (Nat. Hist.). Mrs. S. A. Malcolm and Mr. R. F. Wise (British Museum (Nat. Hist.)) have both given valuable technical assistance in the preparation of this paper.

Mr. M. Mitchell (Institute of Geological Sciences, London) and Dr. G. F. Elliott have kindly read and criticized the palaeontological and stratigraphical sections of the manuscript respectively.

III. STRATIGRAPHY

A detailed account of the Devonian stratigraphy of south-east Devon is outside the scope of this work. As the vast majority of the material described comes from only six localities, however, it is intended to give a brief account of them here. They are confined to the limestones in the Torquay, Paignton and Newton Abbot areas (see Text-figs. 1, 2). Further general information on the geology of south-east Devon can be obtained from the Geological Survey Memoirs (Ussher 1903; Ussher *et al.* 1913; Lloyd 1933).

(a) Middle Devonian.

Dyer's Quarry (SX 92206280) is situated in the coastal cliffs at the western end of the Daddy Hole limestone mass. Exposed to sea level in the floor of the disused quarry is a 15 ft. sequence of thin-bedded, black, crinoidal limestones exceedingly rich in coral remains, overlain by virtually unfossiliferous limestones becoming lighter in colour and more massive towards the top of the quarry. The total thickness of exposed rock is about 60 to 70 ft.

The coral fauna in the floor of the quarry was mentioned briefly by Scrutton (1965 : 186) who suggested for it a lower Middle Givetian age. It is dominated by colonies of *Thamnophyllum germanicum schouppei* nom. nov. (see p. 120), relatively unbroken and apparently preserved in their position of growth. Some of the simple corals also appear to retain their growth orientation. This suggests a sheltered environment, either protected from, or situated below the effects of strong wave action, as the large slender branching colonies of *Thamnophyllum* must have been rather delicate structures during life. The horizon with abundant *Thamnophyllum* is sharply succeeded by dark limestones with few solitary corals. Just above the junction is a thin band containing rounded limestone pebbles which probably represents contemporaneous erosion of the sea floor by wave action.

Wolborough Quarry (SX 85237042), in the south-west outskirts of Newton Abbot, has produced a large and varied fauna of Middle Devonian aspect in the past (Whidborne 1888–1907; Ussher *et al.* 1913 : 22–24) although corals have received little mention. Today, however, it is badly overgrown and the accessible outcrops yield only scattered fossils. The quarry is cut in massive, irregularly jointed limestones, usually coarsely crystalline, with a considerable bioclastic content and variously coloured from dark grey to a very pale yellowish tint.

Phillipsastrea devoniensis (Edwards & Haime) has been recorded from Wolborough and *Billingsastraea? battersbyi* (Edwards & Haime) (see Scrutton 1967 : 277) seems to have been fairly common there in the past. *Phillipsastrea hennahi hennahi*, a single specimen, and *Thamnophyllum caespitosum* (Goldfuss) have now been collected from the quarry together with scattered solitary corals including *Stringophyllum* sp.

The exact stratigraphical position of the Wolborough limestone was held to be uncertain by Ussher *et al.* (1913), but House (1963 : 5) has shown that the *Maenioceras molarium* Zone of the middle Givetian is well developed here. Middleton (1959) unfortunately did not describe Wolborough representatives in his paper on south Devon tetracorals, but later (1960, table 1) he gave a general stratigraphical table for the Newton Abbot area based on a modified version of Wedekind's coral zones. It appears that the Wolborough limestone belongs to Middleton's Givetian "biostromal and clastic limestones" unit, separated, at least in part, from the "biohermal Frasnian limestone" of Ramsleigh Quarry and elsewhere by tuffs.

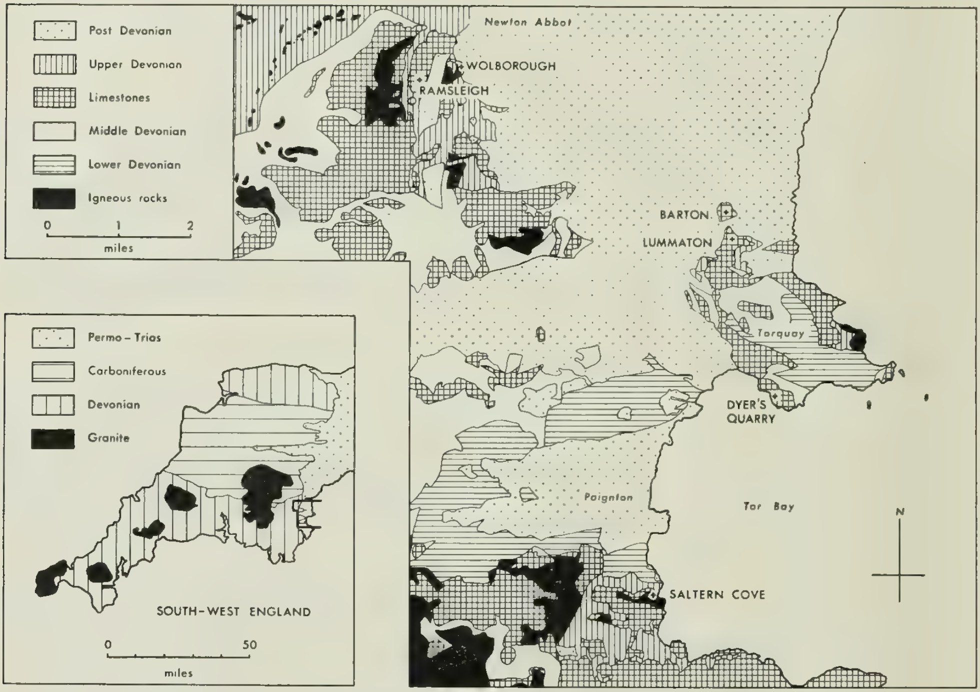

Post Devonian
Upper Devonian
Limestones
Middle Devonian
Lower Devonian
Igneous rocks
0
1
2
miles
Newton Abbot
WOLBOROUGH
RAMSLEIGH
BARTON
LUMMATON
Torquay
DYER'S QUARRY
Paignton
Tor Bay
N
SALTERN COVE
Permo – Trias
Carboniferous
Devonian
Granite
SOUTH-WEST ENGLAND
0
50
miles

FIG. 1. Geological map of south-east Devon showing the main collection sites thus +. Inset map shows the position of the area (based on Geological Survey maps).

Lummaton Hill (SX 91306645). Probably more has been written about the series of quarries now within the northern outskirts of Torquay, than any other Devonian limestone exposure in the country. An early account of the lithologies and faunas in the quarries was given by Jukes-Browne (1906). Despite the massive nature of the limestones, and the undoubted, though obscure, structural deformation, he suggested that a definite lithological succession could be established. Most of the lithological types—the massive stromatoporoid limestone, the grey shelly limestone of the Lummaton Shell Bed, and the bioclastic limestone of the more northern exposures—can still be recognized today. The rich and varied Lummaton fauna derives mainly from the Shell Bed and was monographed by Whidborne (1888–1907). The latter did not mention corals, but Jukes-Browne recorded *Phillipsastrea hennahi hennahi* and *Haplothecia pengellyi* (Edwards & Haime) from the bioclastic limestones in the northern end of the western quarries and noted that they did not occur elsewhere at Lummaton. Unfortunately, this particular locality has been worked out and these corals can no longer be collected here. They are still to be found, however, in limestones of a similar lithology exposed in nearby Barton Quarry.

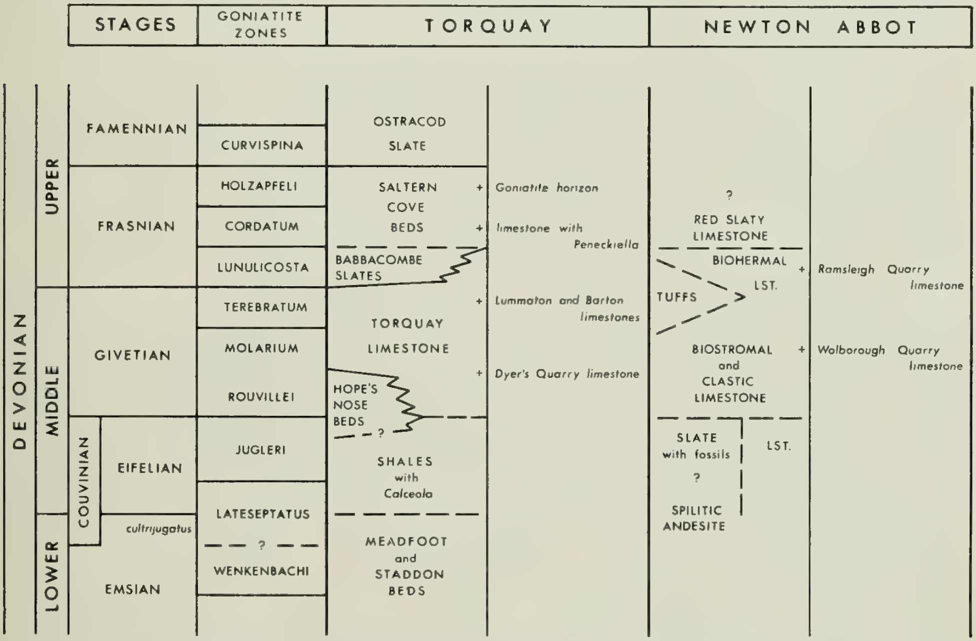

STAGES
GONIATITE ZONES
TORQUAY
NEWTON ABBOT
DEVONIAN
UPPER
MIDDLE
LOWER
COUVINIAN
FAMENNIAN
FRASNIAN
GIVETIAN
EIFELIAN
EMSIAN
cultrijugatus
CURVISPINA
HOLZAPFELI
CORDATUM
LUNULICOSTA
TEREBRATUM
MOLARIUM
ROUVILLEI
JUGLERI
LATESEPTATUS
?
WENKENBACHI
OSTRACOD SLATE
SALTERN COVE BEDS
BABBACOMBE SLATES
TORQUAY LIMESTONE
HOPE'S NOSE BEDS
?
SHALES with Calceola
MEADFOOT and STADDON BEDS
Goniatite horizon
limestone with Peneckiella
Lummaton and Barton limestones
Dyer's Quarry limestone
?
RED SLATY LIMESTONE
BIOHERMAL
LST.
TUFFS
BIOSTROMAL and CLASTIC LIMESTONE
SLATE with fossils
LST.
?
SPILITIC ANDESITE
Ramsleigh Quarry limestone
Wolborough Quarry limestone

FIG. 2. Devonian successions for the Torquay area (modified after House & Selwood 1965) and the Newton Abbot area (modified after Middleton 1960).

Recent quarrying near the supposed strike of the Shell Bed has exposed a grey limestone with scattered brachiopods, tabulate and simple rugose corals, bryozoa and broken colonies of *Thamnophyllum caespitosum paucitabulatum* subsp. nov. This is the first record of *Thamnophyllum* from Lummaton. The lithology suggests that the horizon is above rather than below the Shell Bed.

The Lummaton fauna was described by Kayser (1889 : 186) as indicative of the upper beds of the Middle Devonian. Recent work has fully substantiated this. Elliott (1961 : 256 *et seq.*) commented on the apparent coexistence of *Stringocephalus* *burtini* and "*Rhynchonella*" *cuboides*, held to be markers for the Givetian and Frasnian respectively on the Continent. This had caused Ussher *et al.* (1913 : 14) to consider the Lummaton limestones to be transitional across the Middle–Upper Devonian boundary. Elliott showed, however, that the "*cuboides*" from the Lummaton Shell Bed should be compared with the Upper Givetian *Hypothyridina procuboides* of Torley (1934) from Germany which strongly suggests a Middle Devonian age for this horizon. House (1963 : 6) later confirmed Elliott's age for the Lummaton Shell Bed. He described a goniatite fauna from this level which can be correlated with the *terebratum* Zone of Upper Givetian age.

Elliott (1961 : 256) quoted the occurrence of *Phillipsastrea hennahi hennahi* at Lummaton and Barton as support for the presence of Frasnian rocks above the Givetian at both localities. Middleton (1959 : 156), however, had already recorded this subspecies from Middle Devonian (? upper *Sparganophyllum* Zone) limestones near Dartington Hall and it is recorded here from undoubted middle Givetian at Wolborough Quarry. Furthermore there is good evidence to suggest an upper Givetian age for the limestones at Barton from which *P. hennahi hennahi* can now be collected.

Barton Quarry (SX 91246710), about a quarter of a mile north of Lummaton, is now used as a caravan camp. The quarry is cut in massive, mainly dark-grey coarse crystalline bioclastic limestone which, in the past, has yielded a large and varied fauna monographed by Whidborne (1888–1907) and listed by Ussher *et al.* (1913 : 26). The former did not record the corals but Ussher *et al.* (1913 : 25) described finer textured parts of the limestone as abounding in corals and stromatoporoids. Most of the corals now seen are tabulates, mainly *Thamnopora* and *Alveolites* but it is still possible to collect a few specimens of *Phillipsastrea hennahi hennahi* and *Haplothecia pengellyi* together with *Acanthophyllum* sp. from the western wall of the old quarry.

Barton is the type locality for *P. hennahi*. The horizon has been considered Frasnian in age based on early Continental records of this subspecies from Upper Devonian rocks. House (1963 : 6), however, has identified *Wedekindella brilonense* (Kayser) from among Whidborne's Barton fauna, presumably coming from the massive limestones of the quarry. This goniatite suggests the *terebratum* Zone and thus an upper Givetian age. In addition *Acanthophyllum* has not so far been recorded above the Middle Devonian. Thus the evidence supports an upper Givetian rather than a Frasnian age for the Barton limestones and on the grounds of lithological and faunal similarity, the beds that in the past yielded *P. hennahi hennahi* and *Haplothecia pengellyi* at Lummaton are probably of the same age.

(b) Upper Devonian.

The disused **Ramsleigh Quarry** (SX 84417015) is situated about a quarter of a mile east of East Ogwell, south-west of Newton Abbot. Exposed in the quarry and in the road cutting immediately to the south are massive, dominantly fine grained limestones, medium to pinky grey for the most part but with prominent lenses of a salmon pink colour.

The age of the Ramsleigh limestones has been considered as Frasnian since the early eighteen eighties at least. Ussher *et al.* (1913 : 15) quoted from an unpublished manuscript written by Champernowne in which the latter considered that the " splendid Ramsleigh mass . . . is precisely the counterpart of the marble masses of the ' Étage de Frasne ' in Belgium ". A few years after Champernowne wrote this, Kayser (1889 : 186) correlated the Ramsleigh limestone with the Ibergerkalk of Germany. In more recent times, Dineley & Rhodes (1956 : 244) investigated a conodont fauna collected from a pale limestone band somewhat below the level in the quarry at which most of the massive corals are found. They concluded that the fauna was Lower Frasnian in age. Middleton (1959) briefly described some of the corals found in the quarry. Under his description of "*Phillipsastraea pentagona* var. *micrommata* " he wrote (p. 157) that " According to Różkowska this variety is characteristic of the upper Frasnian ". It is presumably on this basis that he considered (p. 156) the Ramsleigh limestone to be " probably middle or upper Frasnian " in age. Różkowska (1953), however, makes no definite statement of the stratigraphical range of this coral, merely describing it from the upper Frasnian of Poland. Furthermore, although *Frechastraea carinata* sp. nov. (= *Phillipsastraea pentagona* var. *micrommata* of authors) does occur at Ramsleigh, Middleton misidentified his material which should correctly be assigned to *F. pentagona minima*. House (1963 : 6), on the evidence of ammonoids collected by Shannon from Ramsleigh Quarry, inferred that the *lunulicosta* Zone, the lowest goniatite zone in the Frasnian, is represented by the massive limestones. Thus the weight of the fossil evidence suggests that these beds are Lower Frasnian in age.

Quite a large and varied collection of massive corals has been made from the quarry and the adjacent road cutting. *Phillipsastrea hennahi ussheri* subsp. nov., *P. ananas* (Goldfuss), *P. rozkowskae* sp. nov., *Frechastraea pentagona pentagona* (Goldfuss), *F. pentagona minima*, *F. carinata* sp. nov., *F. goldfussi* (de Verneuil & Haime) and *F. bowerbanki* (Edwards & Haime) are described in this paper and *Haplothecia ogwellensis* Scrutton elsewhere (Scrutton 1967 : 272). Most of the material recently collected came from the higher parts of the old quarry face and from a series of outcrops in the road cutting, between 20 and 80 yards west of the lane leading to the quarry.

Saltern Cove (SX 895585), on the shores of Tor Bay, is 1½ miles south of Paignton. Resting on the altered doleritic rock, variously interpreted as a lava or a sill, which forms the southern horn of the cove, is a sequence of shales and limestones of Upper Devonian age (see Lloyd 1933 : 86 *et seq.*; House 1963 : 8; Scrutton 1965 : 188). Immediately above the igneous rock is about 20 ft. of thick bedded limestone with a distinctive band rich in broken colonies of *Peneckiella* at the base (SX 89505842). This is the " main *Peneckiella* horizon " referred to elsewhere in this paper. Higher in the succession intercalations of red shale become increasingly important, separating thinner beds of limestone which completely disappear some 50 ft. above the base of the sequence. The corals in these thin bedded limestones have been briefly mentioned by Scrutton (1965 : 188) as indicating a Frasnian age. With the presence of the *holzapfeli* Zone of Upper Frasnian age established in the northern end of the cove, the limestone horizons are probably within the Middle Frasnian *cordatum* Zone as inferred by House (1963 : 7–8).

IV. GENERAL PALAEONTOLOGY OF THE COLONIAL PHILLIPSASTRAEIDAE

Features of the microstructure, increase and variation in the Phillipsastraeidae are sufficiently uniform to warrant general treatment. By so doing much repetition is saved in the systematic descriptions of individual species and subspecies. The terminology used in this and subsequent sections is that given by Moore, Hill & Wells (1956) unless otherwise indicated.

(a) Microstructure.

Slight recrystallization or deformation of coral material may easily obscure the details of fine structure in the skeletal tissue. Although the preservation of the English Devonian material is not particularly good, all the species and subspecies described here do show some details of their original microstructure.

The septa are characterized by a dark, irregular median line on either side of which are fibres of crystalline calcite (see for example Pl. 13, fig. 1). Where the preservation is best, the fibres can be seen arranged in paired tufts or fascicles on either side of the septal axis. Each pair is presumably the cross-section of a single monacanthine trabecula, with the successive centres of calcification in the fibre fascicles, and thus in the trabecular axes, forming the dark median line. It has not been possible, however, to distinguish clearly the boundaries of individual trabeculae in cross-section.

The structure is most clearly developed in the dilated part of each septum, in the zone immediately outside the tabularium. The dilatation appears to be the result of simple swelling of the trabeculae. There is never more than a slight offsetting of the centres of calcification—in other words, very little break-up or zigzagging of the dark median line—to suggest that the septa become multitrabecular.

The arrangement of the trabeculae in the vertical plane is reflected by the direction of divergence of the fibre fascicles from the median plane of the septum in cross-section (see Kato 1963, text-fig. 3). In the phillipsastraeids described here, the fibres can sometimes be clearly seen changing their attitude to face outwards at either end of the dilated part of the septum, corresponding to the fan-shaped divergence of the trabeculae in the septal plane. The point of divergence is located more or less centrally in the zone of septal dilatation.

The carination developed in *Frechastraea carinata* sp. nov. and *Peneckiella salternensis* sp. nov. is due to the development of regularly spaced, enlarged trabeculae. Whilst the trabeculae retain their linear arrangement along the septal axis the carinae are yard-arm, but they may become offset on alternate sides of the septum, resulting in xyloid carination. The swollen trabeculae are sometimes separated by clear structureless calcite as though the trabeculae had separated and the septa become discontinuous. To what extent this effect is the result of recrystallization is difficult to ascertain.

In longitudinal-section, the arrangement of the trabeculae in the septal plane can often be clearly seen (Text-figs. 3, 7*b*). As mentioned above, the trabeculae are arranged in a fan and this is centred on the crest of the dissepimentarium, usually formed by horseshoe or peneckielloid (Różkowska 1960 : 32) dissepiments. In the zone of septal dilatation, which is most frequently sectioned in a longitudinal slice, the trabecular fan may often appear symmetrical about the axis of divergence. When more rarely a longitudinal-section is obtained of the thinner parts of the septum, the symmetrical arrangement is not maintained. Particularly in the species of *Phillipsastrea* and *Frechastraea*, the trabeculae in the dissepimentarium gradually return to a vertical position as the septa are traced towards the periphery of the corallites. In the tabularium, septa are composed of trabeculae from the edge of the fan, entering from the dissepimentarium at a very low angle, often almost horizontally. The attitude of the trabeculae appears always to be normal to the dissepimental surface (Text-fig. 3).

In the case of *Thamnophyllum* (Text-fig. 7*b*), the evidence suggests that the trabecular fan is more nearly symmetrical in the septum although, in the major septa particularly, the centre of divergence is closer to the epithecal than the axial end. The fan in species of *Peneckiella* is somewhat less symmetrical and more variable in shape—a reflection of the diversification in dissepimental form.

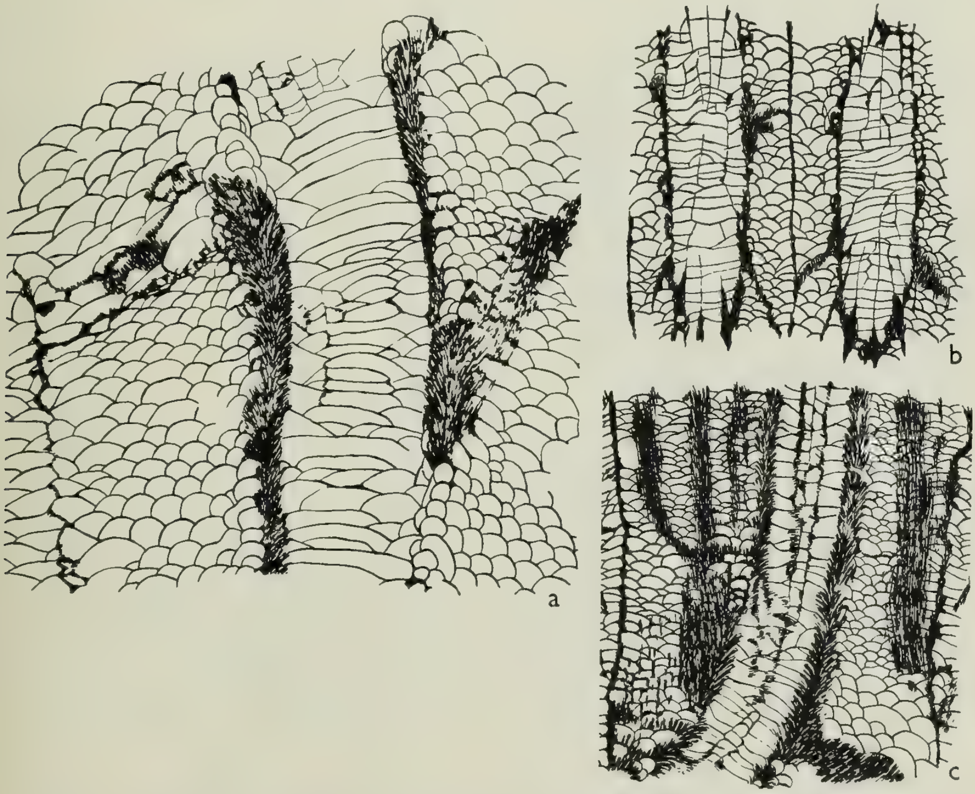


Fig. 3. Comparative longitudinal-sections: *a. Phillipsastrea hennahi hennahi* (OUM D520/p2); *b. Frechastraea pentagona pentagona* (OUM D537/p2); *c. Frechastraea carinata* (OUM D310b). All ×8.

In the massive species described here, the septa are either more or less confluent between corallites (e.g. *Frechastraea bowerbanki*) or intermingle to form a pseudotheca. The rôle of individual septa is usually clear in the formation of a diffuse and irregular pseudotheca such as that in the astraeoid *Phillipsastrea hennahi* (Text-fig. 4*c*). In some species of *Frechastraea*, however, the peripheral ends of the septa are sharply geniculate and form a very strong wall by their fusion with one another (Text-fig. 4*b*). The part played by the individual septa is not clear although the septal characteristics of the pseudotheca are obvious. In *Frechastraea carinata*, carinae may be rarely seen on the pseudotheca where the septal carination has been carried over into the wall. In the past, massive corals with such walls have been called cerioid (Różkowska 1953 : 62) but this term should be strictly confined to massive corals in which an epitheca still surrounds individual corallites (Text-fig. 4*a*) (Lang 1923 : 123; Hill 1935 : 488). Thus the term **" pseudocerioid "** is introduced here to describe such corals as *Frechastraea pentagona pentagona*, *F. carinata* and *F. goldfussi* in which a strong pseudotheca is built up by modified septal elements.[1]

---

[1] See Addendum.

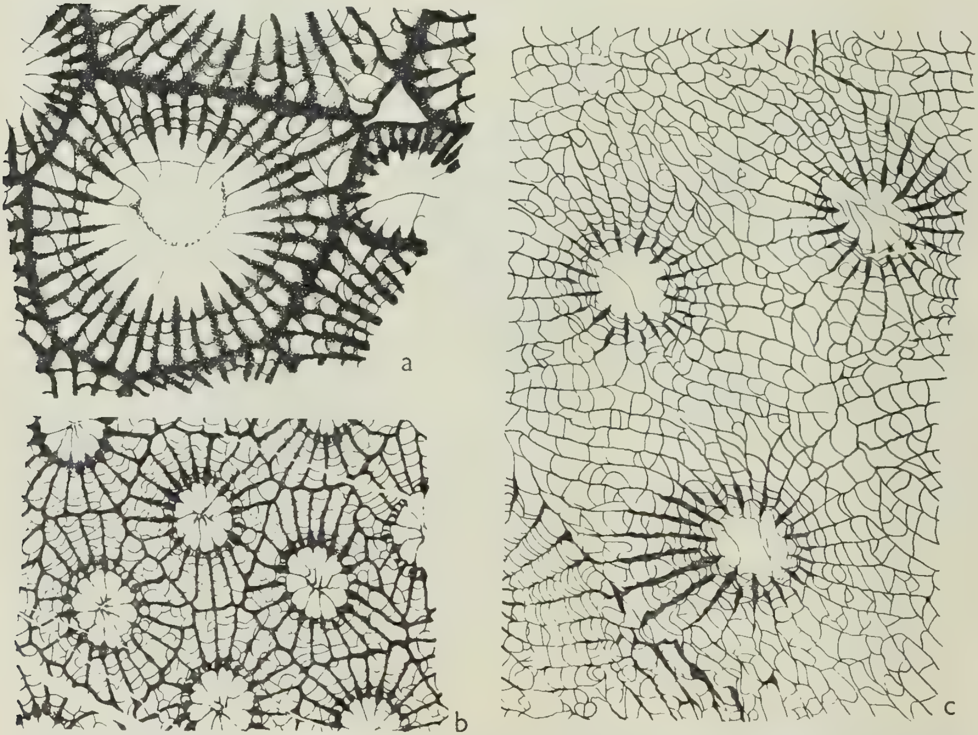


Fig. 4. Comparative wall structures: *a.* cerioid—*Hexagonaria firthi* (BM(NH) R29476); *b.* pseudocerioid—*Frechastraea goldfussi* (OUM D539/p2); *c.* weak astraeoid—*Phillipsastrea hennahi hennahi* (OUM D520/p 1). All ×5.

All the massive coralla described here are presumably surrounded by a holotheca (Hill 1935 : 497) although it has only been observed in *Frechastraea micrommata* (C. F. Roemer) and in two sections of *F. goldfussi*. It is fibronormal in character and somewhat variable in thickness in the range 0·1–0·15 mm. Both the septa and the pseudotheca abut with a shallow convex surface against the holotheca, or penetrate slightly to form a wedge-shaped depression in its surface.

Thamnophyllum germanicum schouppei, *T. caespitosum*, *T. caespitosum paucitabulatum* and *Peneckiella salternensis* have cylindrical corallites with fibronormal epithecae. The peripheral septal ends meet the epitheca and depress it slightly (Kato 1963, text-fig. 17*f*) in the same manner as the relationship between septa and holotheca in *F. goldfussi*.

In all cases where the microstructure can be distinguished, the tissue of dissepiments and tabulae is fibronormal.

(b) Increase.

For full details of corallum increase it is necessary to cut serial sections but in the present material, this has been possible only with *Thamnophyllum germanicum schouppei*. Even in this subspecies, fracturing has so affected the point of branching that the details of septal insertion are obscured. Increase in the other taxa described here is known only from random sections cut through developing or immature individuals. Both axial and lateral increase are recorded and in some cases both may occur within the same colony.

At the present time no detailed work has been done on increase in plocoid rugose corals. Most of the methods of increase observed in the present material, however, have been briefly described by Różkowska (1953). The most common process is the development of one or more new individuals in the border area of two or more surrounding adult corallites (Text-figs. 5*a*, *b*). Różkowska (1953 : 39, 71) called

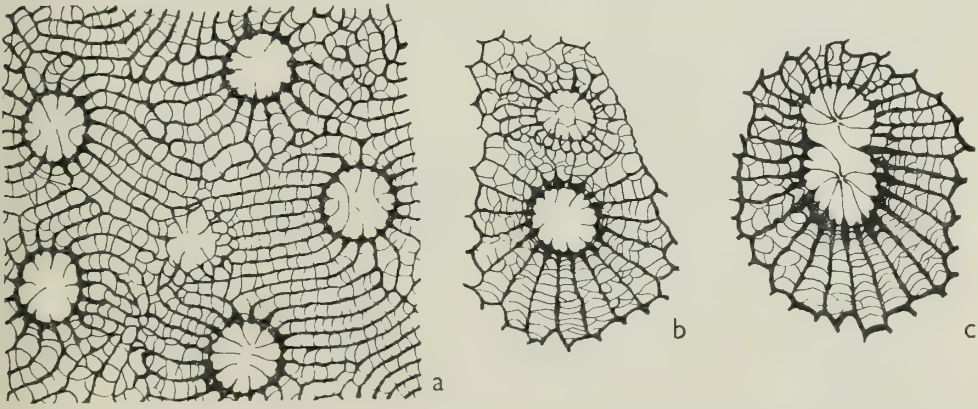


Fig. 5. Increase in massive Phillipsastraeidae: *a*. lateral (intercalicinal)—*Frechastraea pentagona minima* (GSM PF4031); *b*. lateral—*Frechastraea goldfussi* (BM(NH) R46370); *c*. axial—*Frechastraea goldfussi* (BM(NH) R46370). 5*a* ×10; 5*b*, *c* ×8.

this " intermural " increase in the case of her " cerioid " colonies and " intercalicinal " increase in the forms she recognized as plocoid. In fact Różkowska's use of cerioid is equivalent to the term pseudocerioid as used here, there being no epitheca but a pseudotheca, formed by modified septal ends separating individual corallites: these colonies are also, therefore, plocoid. Intermural increase was defined by Hill (1935 : 491) in terms of truly cerioid coralla and it was further restricted by Jull (1965 : 206) to daughter corallites which appear to develop between corallite walls without a particular parent. In view of the literal meaning of " intermural ", Jull's definition is accepted here as it is within the original scope of the term and is most suitably described by it. Różkowska's " intermural " increase (Różkowska 1953 : 71 did mention that the term was not altogether appropriate) is better considered as a form of lateral increase. In some instances (Text-fig. 5*b*), the daughter corallite appears to develop in a very similar manner to that described as lateral in the cerioid *Lithostrotion* cf. *portlocki* by Jull (1965, text-fig. 6(1)). More usually in these pseudocerioid corals, however, the daughter corallite has no wall separating it from most, if not all, of the surrounding corallites during the early stages of development and the parent corallite may be very difficult to distinguish (see Różkowska 1953, text-fig. 35). This latter situation seems not to differ fundamentally from intercalicinal increase in the other plocoid corals with weak or absent corallite walls (for example Text-fig. 5*a* and Różkowska 1953, text-fig. 25). It is proposed, therefore, to term both the intermural and intercalicinal increase of Różkowska (1953) as lateral increase. Full understanding of these processes in plocoid coralla, however, must await studies by serial sectioning.

Examples of axial increase have been seen much more rarely in the massive corals (Text-fig. 5*c*). Consequently, knowledge of the process is based on very few sections and cannot be described in full. Increase is apparently effected by the elongation and subsequent bilobation of the tabularium with commensurate insertion of new septa. The parent tabularium finally divides into two new individuals and their full rings of septa are completed in the area of fission. In all of the few examples seen there are never more than two new individuals formed at the same time.

Axial increase has been recorded in three massive species, all of which have predominant lateral increase (Table 1).

The process interpreted as " axial increase " by Różkowska (1953 : 65, text-fig. 39) in her " *Phillipsastraea pentagona* " has also been observed in several specimens among the present material. From Różkowska's figure and a consideration of the English specimens, however, it is doubtful whether this is really increase but rather a form of rejuvenescence in massive coralla. There is no indication that this phenomenon ever leads to the formation of two or more individuals. Confirmation of this interpretation must nevertheless await evidence from serial sectioning.

Mode of increase in the massive corals is summarized below (Table 1). It is possible that axial increase may be shown to occur in other species than those indicated when more material has been examined.

Of the phaceloid corals described here, one has exclusively axial increase and the others, exclusively lateral.

Thamnophyllum caespitosum and *Peneckiella salternensis* have a style of increase

TABLE 1.—Increase in massive Phillipsastraeidae.

	Lateral	Axial
Phillipsastrea		
P. hennahi hennahi	×	
P. hennahi ussheri	×	
P. devoniensis	No evidence	
P. ananas	×[1]	
P. rozkowskae	No evidence	
Frechastreaea		
F. pentagona pentagona	×	×
F. pentagona minima	×	×
F. micrommata	×	
F. carinata	×	×
F. goldfussi	×	×
F. bowerbanki	×	

[1] After Frech, 1885, pl. 2, fig. 5.

similar to that described as " thamnophylloid lateral " by Różkowska (1960 : 31). The daughter corallite arises from the dissepimental tissue of the parent (Text-figs. 6, 7). In the early stages, the adult corallite becomes egg-shaped in cross-section with the more pointed end containing dissepimental tissue only, the septa having withdrawn from the epitheca in this area. This projection expands in size and septa begin to appear on the wall farthest from the parent. Some septa from the parent itself may extend slightly into the developing individual where the two are joined and these appear eventually to contribute to the latter's full complement of septa. As the process continues, the daughter corallite grows more circular and forms a bilobed complex with the parent. At the same time, new septa are inserted on

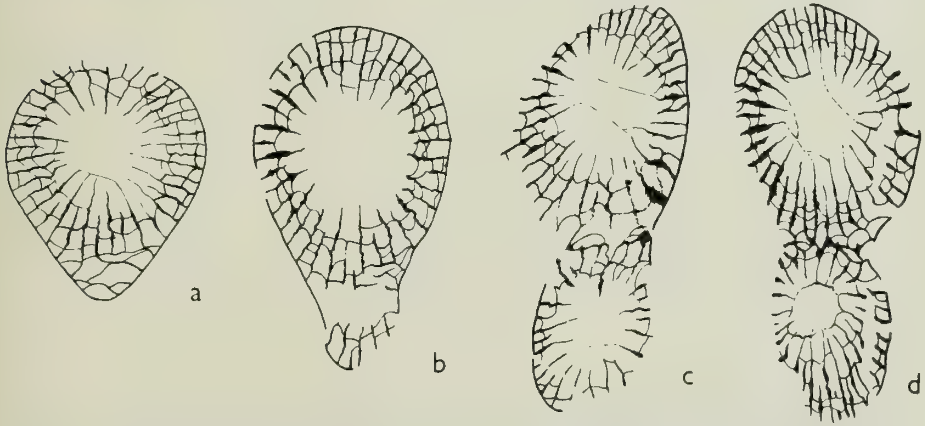


FIG. 6. Lateral increase in *Peneckiella salternensis*: *a*. OUM D553/p1; *b*. OUM D547/p1; *c*. OUM D547/p3 (same corallite as in 6*b*); *d*. OUM D553/p1. All ×5.

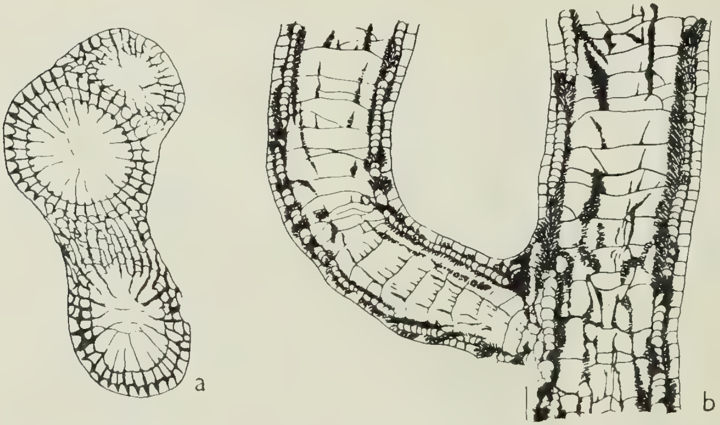


FIG. 7. Lateral increase in *Thamnophyllum caespitosum paucitabulatum*: *a.* BM(NH) R46162*d*; *b.* BM(NH) R46163*d*. Both ×3.

both flanks of the daughter which now possesses most adult characteristics. During the bilobed stage, the two calices are wholly or partially separated by an irregular pseudotheca formed by the geniculation and mutual interference of the septa in the waist of the complex. The daughter corallite may be connected to the parent by extra-dissepimental tissue before final separation when the latter's epitheca may be complete. In *Thamnophyllum caespitosum* two daughter corallites may be produced at the same level but this has not been observed in *Peneckiella salternensis*.

Thamnophyllum germanicum schouppei on the other hand displays exclusively axial increase similar to that found in many other species of *Thamnophyllum*. In all the specimens examined, either three or four daughter corallites are produced in each case. One specimen, in which increase is threefold, has been serial sectioned (Text-fig. 8). The parent corallite is about 5 mm. in diameter at the inception of increase which is marked by a striking change in skeletal deposition in the tabularium. After the last normal tabulae are laid down in the parent, the dissepimentarium continues to form as usual. In the tabularium, however, steeply inclined plates are secreted to form a cone (Text-fig. 8iii) which modifies upwards into a pyramid with as many sides as daughters are produced (Text-fig. 8iv, v). Upon these plates the new individuals are built up. As the cross-section of this axial structure changes in threefold increase from circular to triangular, three septa, each opposite and extending to join a corner of the triangle, become increasingly strongly developed. These delimit the areas of the new corallites. Thus each new corallite inherits roughly a third (or in fourfold increase, a quarter) of the mature septa and dissepiments of the adult. The first tabulae of each daughter are deposited between the base plate and the inherited dissepiments. Meanwhile the cross-section of the complex becomes increasingly trilobed (or tetralobed) and new septa are inserted along the inner margins of the developing corallites (Text-fig. 8vi, vii). The formation of the

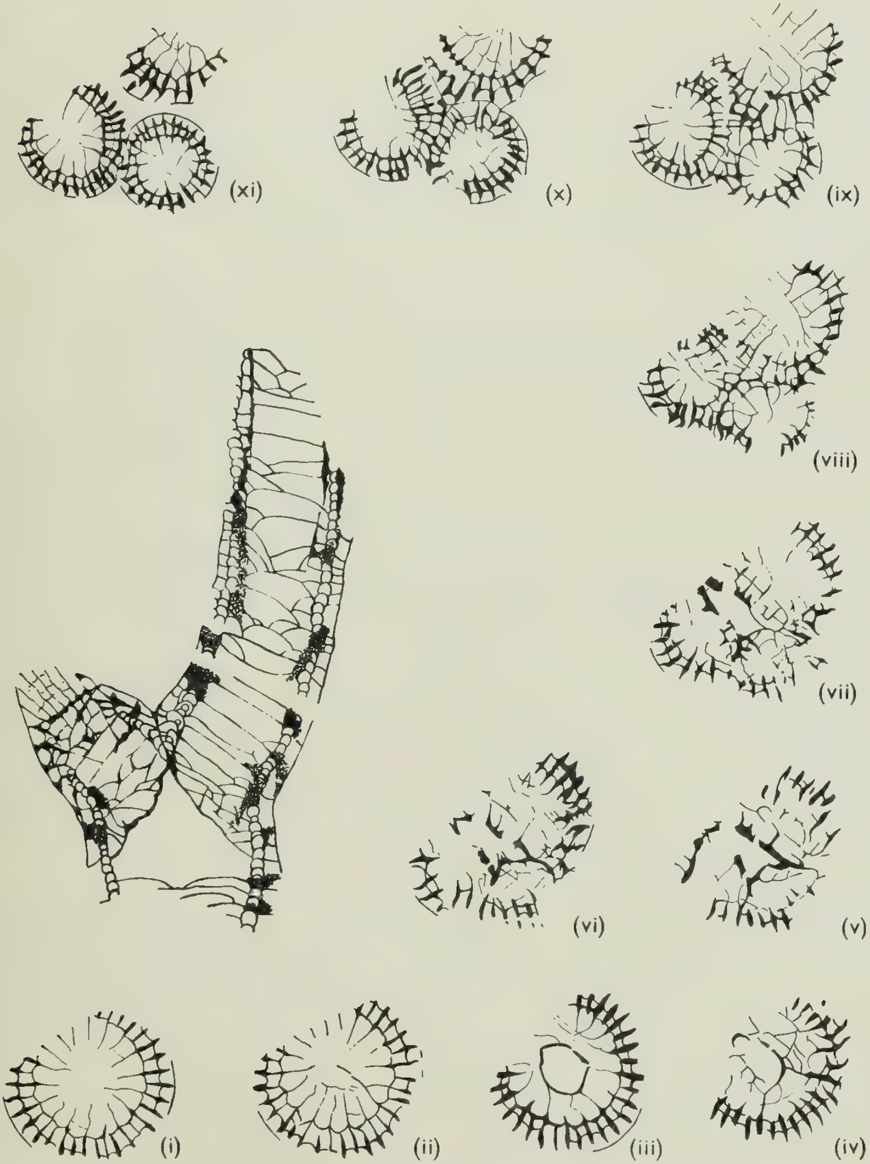


FIG. 8. Axial increase in *Thamnophyllum germanicum schouppei*: longitudinal-section after OUM D272; serial cross-sections after OUM D510/p5–10, p12–16. Spacing of sections in mm: i(p5)—0·747—ii(p6)—1·126—iii(p7)—0·712—iv(p8)—0·444—v(p9)—0·330—vi(p10)—0·533—vii(p12)—0·208—viii(p13)—0·267—ix(p14)—0·495—x(p15)—0·574—xi(p16). All ×5.

new horizontal structural elements proceeds from the periphery towards the axial area of the complex and by the time the process is close to completion, vertical growth has passed the apex of the base plates and the daughters are in intimate contact (Text-fig. 8viii). Subsequently, the newly formed sections of the dissepimentaria acquire adult characteristics with distinct traces of horseshoe dissepiments in cross-section (Text-fig. 8ix, x) and the new corallites complete their epithecae. Evidently no extra-dissepimental tissue (caenogenetic tissue of Soshkina 1953) is formed in *Thamnophyllum germanicum schouppei*, for as soon as the normal dissepimental tissue is developed, the daughters become phaceloid (Text-fig. 8xi).

(c) Variation.

(i) Introduction. Sufficient material is available of many of the taxa described here to allow their variation to be studied in some detail. The statistics are grouped with the individual species and subspecies as part of their characterization but their great interest is in the general trends they show which are commented upon here.

There are certain problems in the statistical treatment of south Devon material. Only one of the samples—*Thamnophyllum germanicum schouppei* from Dyer's Quarry—is demonstrably from a population preserved more or less in position of growth. In all other cases the faunas from which collections have been made have apparently suffered some post-mortem movement, the extent of which is difficult to assess. The coral colonies are broken and disorientated, in most cases preserved in massive limestones which have suffered more or less from tectonic stresses and recrystallization.

The collections thus consist of fragmentary coralla which preclude ontogenetic study. The influence of ontogeny on the data obtained from these corals, however, appears to be small. Longitudinal-sections of corallites in the massive colonies show tabularium diameters to be virtually constant over most of their vertical growth. In this respect, they appear to behave in the same way as the phaceloid colonies, in which the influence of ontogeny is minimal in the extensive cylindrical parts of the corallites.

All measurements have been made in cross-sections. In many colonial corals, a large number of corallites are unavoidably cut at varying degrees of obliquity, resulting in elliptical sections. As the corallites in the phaceloid colonies and the tabularia in all the colonial corals considered here are circular in sections normal to their axes, diameter measurements have been made along the minor axis of the ellipse. Care has been taken to separate ellipticity due to oblique section from that resulting from crushing or tectonic distortion. Corallites which appear to have been deformed in this way have not been measured.

The following dimensions were recorded for each corallite:

d	**corallite diameter.** Measured only in phaceloid colonies and recorded to the nearest 0·1 mm.
dt	**tabularium diameter.** All of the corals described here have a clearly defined tabularium junction: recorded to the nearest 0·1 mm.
n	**number of major septa.** Counts of the number of major septa were recorded with the corresponding **d** and/or **dt** value.

The following were calculated in the case of all massive coralla:

A	**average corallite area in a colony.** As it is not possible to measure corallite diameter in a massive colony, the average corallite area in a colony was measured to facilitate comparison of corallite and tabularium size. Values of **A** were obtained by counting corallite numbers in a cross-sectional area measured by means of a transparent graticule divided into squares of 0·5 cm. side. The number of corallites was then divided into the corresponding area and the result recorded in square centimetres. Care was taken to calculate **A** from those corallites whose tabularia were also measured. This value is subject to some error due to the inclusion in its calculation of some obliquely sectioned corallites.
At	**average tabularium area in a colony.** Calculated from **dt$\bar{x}$** (the mean tabularium diameter) of each colony by the formula for the area of a circle and recorded in square centimetres.

From the above basic data, the following ratios were calculated:

dt/d	**tabularium, corallite diameter ratio.** This ratio could only be calculated for phaceloid colonies.
n/d or **n/dt**	**septal** or **septal-tabularium ratio** respectively. The septal ratio as normally applied to corals is the number of major septa divided by the corresponding corallite diameter, which in the present work could only be calculated for the phaceloid colonies. In the massive corals, the ratio of the number of major septa to the tabularium diameter, called the septal-tabularium ratio, was calculated. This ratio behaves in a similar way to the septal ratio but is not directly comparable with it. It will, of course, have higher values than corresponding septal ratios and may vary differently with size, depending on the variation in the **dt/d** ratio.
At/A	**tabularium to corallite area ratio.** This ratio is the approximate counterpart in massive corals of the **dt/d** ratio in phaceloid corals. The **At/A** ratio, however, has only been calculated as an average for each colony and not for individual corallites because of the difficulty of measuring accurately the area of an irregularly polygonal corallite.

For the dimensions and ratios mentioned above, the following standard statistics were calculated:

N	**sample size.** The number of corallites in the sample, with the number of colonies given in parentheses. In the case of **A**, **At**, and the ratio **At/A**, **N** is the number of colonies.
O.R.	**overall range.**
$\bar{x}$	**mean value.**
s	**standard deviation.**
C.V.	**coefficient of variation.**
S.E.$_m$	**standard error of the mean.**

These elementary statistics are dealt with in many books and their application to zoology and palaeontology is discussed in Mayr, Linsley & Usinger (1953) and

Simpson, Roe & Lewontin (1960). Reference has been made to both these texts during the present work but principally, the writer has followed Imbrie (1956). The latter gives a clear and concise account of all the biometric techniques used here. It was found necessary, however, in view of the large size of most of the samples, to calculate the statistics for all characters except **A**, **At** and **At/A** by grouping the data in class intervals corresponding to the 0·1 mm. intervals in which the diameters were measured.

The statistics calculated for each species and subspecies and the representative colonies are given in tabular form with the systematic descriptions (Tables 4–16). The colonies selected for individual treatment were those in which the most corallites could be measured. Usually it was possible to use colonies with 50 or more corallites but in cases of species with large calices, smaller numbers had to be used. The colony with the least data is Colony 1 of *Thamnophyllum germanicum schouppei* with 23 measured corallites.

The data are also illustrated graphically (Text-figs. 9–21). In the plots of **dt** against **d**, **n** against **d** or **dt**, **n/d** against **d** and **n/dt** against **dt**, diameter is recorded along the abcissa to the nearest 0·1 mm. As stated above, the character on the ordinate was averaged and plotted as a single point in each 0·1 mm. class. Thus points in the middle of the ranges of values on these graphs were based on many more observations than those at either end.

On all the graphs, the scatter of points approximated fairly closely to a straight line. When similar graphs are plotted for complete ontogenetic studies, it has been shown that the points usually fall on a curve of quite complicated form (see Voynovskiy-Kriger 1954). In the present case, however, the influence of ontogeny is thought to be slight and the data representative of the mature growth stages. Voynovskiy-Kriger's curves approximate very closely to straight lines in maturity (his "mature" plus "old" stages), as is shown by the present results. Thus straight lines have been calculated from the data represented by the scatter of points on each graph. For ease of comparison, the lines only are illustrated in the text-figures. After Imbrie (1956), the reduced major axis was chosen as the most suitable line for problems of relative growth.

For each line, the formula is given in the data tables as follows:

r correlation coefficient
a " growth ratio " } line of the form $\mathbf{y} = \mathbf{ax} + \mathbf{b}$
b " initial growth index " }

Where statistical discrimination has been used between congeneric species and subspecies, the procedure followed is again that detailed by Imbrie (1956).

(ii) Variation in diameters. The assessment of size in these corals is mainly through the analysis of tabularium diameters as corallite diameters can only be measured in the phaceloid colonies. Variation in size may be the result of genetic, ontogenetic or ecological influences. Because of the parts played by the latter two factors, which are often not easy to assess, care must be taken in the significance placed on size differences and relative variation between colonies and species. In the present case, ecological control is largely an unknown factor although the influence of ontogeny may be regarded as minimal.

The variation in tabularium diameter in each of the taxa considered here is fairly similar (see Table 2). Values of **C.V.** range from 7·73 for the sample of *Frechastraea bowerbanki* to 14·79 for the sample of *Thamnophyllum germanicum schouppei*. Variation in the former, however, is almost certainly underestimated as only four incomplete colonies were available for measurement. Values of **C.V.** for the other species of *Frechastraea* are all about 10. These figures are close to those obtained by Oliver (1960 : 83, table 7) for solitary cylindrical coral species and much lower than the variation he found in conical forms.

From the present data it is impossible to say if massive corals are more or less variable than phaceloid forms. Although *Thamnophyllum germanicum schouppei* has the highest **C.V.** value, those for *T. caespitosum paucitabulatum* and *Peneckiella salternensis* are much the same as the values for many of the massive corals. In fact, the **C.V.** figure for the Barton Quarry sample of *Haplothecia pengellyi*, a massive marisastrid (see Scrutton 1967 : 274, table 2), is 15·75, which is higher than that for *T. germanicum schouppei*. On the other hand, there is a general tendency for **C.V.** values to be higher with increase in mean tabularium diameter. In the phaceloid corals, variation in corallite diameters is roughly the same from species to species, although always lower, than in the corresponding tabularium diameters. Oliver's results with six solitary corals do not show such consistency and tabularium diameters are less variable than corallite diameters in two instances.

Variation in size within colonies, with only two exceptions, was found to be less than that in the total samples of the same species or subspecies from the same locality. One exception is Colony 1 of *Frechastraea bowerbanki* (Table 12) which species has already been explained to be probably inadequately sampled. The other exception is Colony 1 of *Phillipsastrea hennahi hennahi* from Lummaton (Table 4). In this case, the **C.V.** value for **dt** in the colony only slightly exceeds that for the total Lummaton sample and is less than that for the sample from nearby Barton.

There is usually a considerable range in the **C.V.** values for colonies of the same species or subspecies, even when the number of measured corallites in each colony is the same or nearly so. This can be illustrated with reference to *Frechastraea goldfussi* (Table 11) in which the **C.V.** values for 10 colonies range from 10·01 to 4·12, the value for the total sample from Ramsleigh Quarry being 10·10.

As coral colonies are ideally the result of asexual reproduction from one sexually produced individual, variation would be expected to be lower in a single colony than in a sample of several colonies. From the results obtained here this is generally substantiated. The wide range in colonial variability may be due in part to several factors. Microenvironmental and general ecological influences undoubtedly exercise some control on variation but their effects cannot be easily assessed. In the case of phaceloid colonies, high **C.V.** values may be the result of the intergrowth of two or more colonies which have been sampled as one. As Oliver (1960 : 74) pointed out, it is virtually impossible to detect intergrowth when collecting material, and this may well have been responsible for the high **C.V.** values in the colonies of *Thamnophyllum germanicum schouppei* (Table 13). Another factor for consideration is the fusion of several sexually produced polyps at an early stage of colony formation,

TABLE 2.—Comparative means and coefficients of variation for all characters and taxa analysed. Species and subspecies are arranged in order of increasing **dt$\bar{x}$.** *F.* = *Frechastraea*; *Ph.* = *Phillipsastrea*; *T.* = *Thamnophyllum*; *P.* = *Peneckiella*.

		F. pentagona minima	*F. carinata*	*F. pentagona pentagona*	*F. goldfussi*	*F. bowerbanki*	*Ph. hennahi ussheri*	*Ph. hennahi hennahi* (Lumm.)	*Ph. hennahi hennahi* (Bar.)	*T. germanicum schouppei*	*P. salternensis*	*T. caespitosum paucitabulatum*
d	**$\bar{x}$**									4·19	5·28	5·68
	C.V.									14·08	10·11	9·66
dt	**$\bar{x}$**	0·96	1·02	1·09	1·53	1·54	2·04	2·32	2·45	2·69	3·51	3·70
	C.V.	10·98	10·56	9·38	10·10	7·73	10·61	10·13	13·27	14·79	10·87	10·88
n	**$\bar{x}$**	9·54	9·75	10·12	11·16	9·54	12·46	12·67	12·92	16·52	19·91	18·92
	C.V.	4·42	3·51	3·15	4·57	2·59	3·07	2·89	3·22	7·41	4·21	3·95
n/d	**$\bar{x}$**									3·98	3·80	3·35
	C.V.									7·51	7·34	8·78
n/dt	**$\bar{x}$**	10·05	9·66	9·36	7·32	6·24	6·16	5·52	5·25			
	C.V.	6·40	7·07	6·34	5·80	5·48	8·97	8·16	11·69			
dt/d	**$\bar{x}$**									0·64	0·67	0·65
	C.V.									2·43	1·68	3·27
At/A	**$\bar{x}$**	0·062	0·063	0·079	0·10	0·054	0·063	0·042	0·045			
	C.V.	12·21	17·68	18·63	17·74	6·13	26·12	17·31	23·41			

recorded in Recent corals by Stephenson (1931 : 124). The effect of this phenomenon would generally be to increase the variation displayed by the colony.

It is very difficult to separate the effects due to these different factors but it seems likely from the wide range in **C.V.** values shown, for example, by the colonies of *F. goldfussi*, that primary polyp fusion could be an important factor.

The investigation of colonial variation described here differs from that made by Oliver (1960 : 73 *et seq.*) through the latter comparing septal ratio **C.V.** values for individual colonies with those for populations of solitary cylindrical corals. In addition, Oliver analysed the total sample of *Tryplasma fascicularia* from colony means rather than the basic corallite data.

(iii) Variation in septal number and the septal ratios. With the exception of *Thamnophyllum germanicum schouppei*, the **C.V.** values for septal number are very similar in all the total samples. There appears to be no relationship between the degree of variation and the mean septal number (Table 2).

It has long been known that septal number depends to some extent on calice size. When one is plotted against the other for both colonies and total samples, **n** shows a general increase with increasing **d** or **dt** in every case. Correlation coefficients in the total samples are usually about 0·9. The figure in individual colonies is slightly lower but much the same from colony to colony. Only rarely does the correlation coefficient drop below 0·7. These figures reflect the strength of the linear relationship between **n** and **d** or **dt** in mature individuals. A correlation between septal number and diameter is still reflected to a large extent in Table 2 as taxa with larger mean diameters have, with few exceptions, greater mean values for **n**.

This relationship had led to the use of the septal ratio (septal coefficient of Voynovskiy-Kriger 1954) as a useful diagnostic criterion in coral species. Różkowska (1957) particularly, has used a form of this ratio, her **Ms**, in a detailed statistical study of species of *Thamnophyllum* and *Macgeea* from Poland. She showed (p. 91 and Table 6) that successively younger species and subspecies of *Thamnophyllum* have lower **Ms** values and similarly, fewer septa at a given diameter. A comparison of Różkowska's figures with the thamnophyllids described here is shown in Table 3.

It can be seen that the **n** values at **d** = 6 mm. for the English material follow the same trend as for the Polish specimens but do not fit exactly into the latter's scale. On the other hand, the English **Ms** values (the English data has been recalculated for direct comparison with Różkowska's figures) are quite different from their approximate age equivalents in Poland and do not fit into a stratigraphical trend. It is interesting, however, to arrange the same taxa in order to increasing mean corallite diameter. This produces a series of decreasing **Ms** values somewhat less perfect than before for the Polish specimens but into which the English figures fit quite well. The values of **n**, however, show somewhat less perfect ordering than when arranged in stratigraphical series.

Turning to the massive corals in Table 2, the mean **n**/**dt** figures for the representatives of *Frechastraea* and *Phillipsastrea* show a perfect series of decreasing values with increasing mean tabularium diameter. Furthermore, just such correlation exists, this time between mean **d** and mean **n**/**d**, in the corals described by Oliver

TABLE 3.—Series in **Ms** and **n** (at **d** = 6 mm.) for English (E) and Polish (P) thamnophyllids. Polish figures from Różkowska (1957 : 91 and table 6).

	Horizon	Name	Country	**Ms**	**n** (at **d**=6 mm.)
Frasnian	Middle	*T. superius*	P	2·20	15
	Lower	*T. kozlowskii*	P	2·30	17
Givetian	Upper	*T. caespitosum paucitabulatum*	E	3·50	19·35
	Middle	*T. caespitosum caespitosum*	P	3·17	20
		(*T. germanicum pajchelae*)	P	(3·60)	(21)
		T. caespitosum	E	3·15	20
		T. germanicum germanicum	P	3·42	21
		T. germanicum skalense	P	3·64	22
		T. germanicum schouppei	E	4·16	20·28

$\bar{x}$ **d**	Name	Country	**Ms**	**n** (at **d**=6 mm.)
4·11	*T. germanicum pajchelae*	P	3·60	21
4·14	*T. germanicum schouppei*	E	4·16	20·28
5·36	*T. germanicum skalense*	P	3·64	22
5·68	*T. caespitosum paucitabulatum*	E	3·50	19·35
(ca.) 6·00	*T. caespitosum caespitosum*	P	3·17	20
6·17	*T. caespitosum*	E	3·15	20
7·00	*T. germanicum germanicum*	P	3·42	21
9·28	*T. superius*	P	2·20	15
10·03	*T. kozlowskii*	P	2·30	17

(1960). Thus the correlation between mean size and mean septal ratio is quite strong. The stratigraphical series in **Ms** values obtained by Różkowska may simply reflect the tendency in her material for larger species and subspecies of *Thamnophyllum* to occur at higher horizons.

Between conspecific colonies, the septal or septal-tabularium ratio behaves in the same way. Colonies with greater mean diameters have, with very few exceptions, smaller values for the mean septal ratio.

This trend is related to the fact that the septal ratio is not constant throughout ontogeny but decreases in value (see Voynovskiy-Kriger 1954) with increasing corallite diameter. When septal ratio is plotted against diameter, the relationship is more or less linear for mature corallites. In the present case correlation coefficients for the total samples range between − 0·90 and − 0·94 for phaceloid and − 0·96 and − 1·0 for massive corals.

C.V. values for septal number and the septal or septal-tabularium ratio in conspecific colonies may show a considerable range. Furthermore, the relative variation in these characters and **d** or **dt** between colonies is usually different, although there is a slight tendency for the colony with the highest **C.V.** value for diameter to have high **C.V.** values for septal number and the septal ratio as well (see for example

Table 11). In the case of **n**, the **C.V.** value reflects to some extent the rate of septal insertion as well as the amount of variation in diameter, and this masks any independent variation in the septal number. Colonies with similar variation in diameter, for example, show a strong correlation between **a**, the growth ratio, in graphs plotting **n** against **d** or **dt** and **C.V.** values for **n**. Similarly, **C.V.** values for **n/d** or **n/dt** in conspecific colonies also correlate roughly with values of **a** for graphs plotting **n/d** or **n/dt** against **d** or **dt**, and inversely with values of **a** for the plots of **n** against **d** or **dt**.

(iv) Variation in size ratios. In the phaceloid forms, tabularium diameter increases evenly with increase in corallite diameter. The relationship between the two is strongly linear, reflected in the high values for the correlation coefficient ($r > 0{\cdot}95$ in all cases). Only three phaceloid colonies have been analysed individually, those of *Thamnophyllum germanicum schouppei*. Their correlation lines on the graph plotting **dt** against **d** are virtually superimposed (Text-fig. 20).

The ratios of tabularium to corallite diameter have very low **C.V.** values, partially reflecting the fact that they are virtually unaffected by changes in diameter. Measurements are confined, however, to mature corallites. Oliver (1960 : 71) has shown that during ontogeny in *Siphonophrentis variabilis* and *Pseudoblothrophyllum helderbergium*, this ratio decreases with increasing diameter. In his analyses of mature individuals, on the other hand, the ratio remains relatively constant with increasing diameter, as is shown in the present material.

The relationship between tabularium and corallite size in massive corals is considered in terms of their respective areas and is restricted to total samples. Analyses of **A**, **At**, and the **At/A** ratio show these characters to have high **C.V.** values. In the same sample there may be a considerable difference between the **C.V.** value for **A** and that for **At**, for example in the case of *Phillipsastrea hennahi ussheri* in which the former figure is more than double the latter (Table 5). This is undoubtedly due in part to the difficulty in calculating accurately the value of **A**. In most cases, however, the two figures are more nearly comparable.

When **At** is plotted against **A**, there is always a clear tendency for the former to increase with increase in the latter (Text-figs. 12, 19). The scatter of points, however, is considerable and is reflected in the low values for the correlation coefficient. Calculations using the formulae for the fitted lines show that the **At/A** ratio may increase or decrease slightly with increasing corallite area. Thus the analyses suggest that this ratio behaves similarly, if not so regularly, as the **dt/d** ratio and is largely independent of size in mature colonies.

V. SYSTEMATIC DESCRIPTIONS

The family name Phillipsastraeidae was erected by Roemer (1883 : 389) to include the genera *Phillipsastrea* and *Pachyphyllum*. It has, however, been little used until recently and taxonomists have usually classified the nominal type genus in the Disphyllidae. Hill (1939 : 224) erected the Disphyllidae to include both the typical *Disphyllum* and the related *Prismatophyllum* (considered by Lang, Smith & Thomas 1940 : 104 as a junior synonym of *Hexagonaria*) as well as *Phillipsastrea* (interpreted by Hill 1939 : 236 to contain species both with and without horseshoe dissepiments) and the exclusively horseshoe bearing genera, *Thamnophyllum*, *Macgeea* and *Trapezophyllum*. Hill's concept of the Disphyllidae was largely influenced by Lang & Smith's (1935) discussion of these genera.

Many subsequent workers followed Hill's combination of horseshoe and non-horseshoe bearing forms in the same family. Stumm (1949 : 31) extended the range of genera included in the Disphyllidae but divided them among three subfamilies, the Pachyphyllinae, Disphyllinae and Eridophyllinae, characterised respectively by the presence and absence of horseshoe dissepiments and the development of an aulos. He considered *Phillipsastrea* to lack horseshoe dissepiments and placed it with *Disphyllum*, *Hexagonaria* and *Billingsastraea* in the Disphyllinae. The Pachyphyllinae included *Pachyphyllum*, *Macgeea*, *Thamnophyllum* and *Trapezophyllum*.

Soshkina (1949), on the other hand, distributed the genera and species here included in the Phillipsastraeidae among three new families on the basis of morphological and ontogenetic considerations. Genera she considered to develop horseshoe dissepiments and a " hexacoralloid " microstructure—*Pachyphyllum*, *Macgeea*, *Thamnophyllum* and *Synaptophyllum*—Soshkina (1949 : 76) grouped in the Thamnophyllidae, equivalent to Stumm's Pachyphyllinae. She placed *Phillipsastrea*, erroneously quoting (1951 : 95) *P. radiata* as type species and interpreting the genus as lacking horseshoe dissepiments, with *Neocolumnaria* and *Schluteria* in the Neocolumnariidae (1949 : 145). The third new family, the Peneckiellidae (1949 : 141) included *Peneckiella* and *Megaphyllum*. The latter was considered by Hill (1956 : 280) to be a synonym of *Disphyllum*.

Soshkina (1951, 1952, 1954) continued to use this classification with the introduction of further genera to the latter two families and (1954 : 44) replacing the name Neocolumnariidae by Neocampophyllidae. Spassky (1960) followed Soshkina's (1954) classification.

Wang (1950 : 217) further enlarged the Disphyllidae by incorporating the acanthophyllids into the family. He based his classification on a consideration of coral microstructure, defining the family chiefly on the development of one or more fan systems in the septal trabeculae. Wang's use of the subfamily Phacellophyllinae (septal trabeculae with a marked area of divergence) corresponds very closely to the scope of the Phillipsastraeidae as interpreted herein. Like Lang & Smith (1935) and Hill (1939), however, he included species both with and without horseshoe dissepiments in *Phillipsastrea*.

Różkowska (1953 : 8 *et seq.*) considered the three different classifications of Stumm (1949), Wang (1950) and Soshkina (1951). She decided that coral microstructure was of particular diagnostic importance and for this reason followed Wang's classification in principle. She did, however, remove the Acanthophyllinae from the Disphyllidae. In addition, she used the subfamily Pachphyllinae *sensu* Stumm in preference to the Phacellophyllinae *sensu* Wang as the former was conceived as exclusive of the genus *Phillipsastrea*. This genus Różkowska interpreted as lacking horseshoe dissepiments and placed in the subfamily Disphyllinae.

Hill (1954*a*, *b*) reintroduced the family name Phillipsastreidae (*sic*) effectively as a senior synonym of her (1939 : 224) Disphyllidae. Although the 1954 papers contain no familial diagnosis, this classification was later given in full by Hill

(1956 : 179). She considered *Phillipsastrea* to lack horseshoe dissepiments and thus placed all the genera with disphyllid and marisastrid dissepimentaria in the Phillipsastraeinae, and the horseshoe bearing genera in the Phacellophyllinae.

Schouppé (1956) discussed at length the classifications of previous authors. He stressed the importance of the so-called " hexacoralloid " microstructure developed in these corals with strongly reflexed dissepimentaria, and advocated their clear systematic separation. Two years later, Schouppé (1958) published a classification on this basis, stressing at the same time the presence of horseshoe dissepiments in the lectotype of *Phillipsastrea hennahi*. He placed all the genera with an area of divergence in their septal trabeculae, usually but not always associated with horseshoe dissepiments, in the Phillipsastraeacea (*sic.*). Thus he elevated what had previously been a family or even a subfamily concept to the level of a suborder.

Schouppé subdivided the Phillipsastraeacea into the Macgeeidae, with subfamilies Macgeeinae and Peneckiellinae, and the Phillipsastraeidae. He placed the genera *Phillipsastrea* and *Billingsastraea* together in the Phillipsastraeidae and listed (1958 : 233) the family characteristics as massive astraeoid form, with a pseudotheca and never an epitheca between adjacent corallites, and with a broad dissepimentarium often developing horseshoe dissepiments. *Phillipsastrea* and *Billingsastraea*, however, are not considered to be closely related (Oliver 1964 : 2; Scrutton 1967 : 276). Furthermore, Schouppé placed *Haplothecia* Frech, *Pachyphyllum sensu* Różkowska (1953) and *Pseudoacervularia sensu* Różkowska (1953) in his synonymy for *Phillipsastrea*, all of which include species with a partial or complete epitheca around some or all corallites. The Macgeeidae *sensu* Schouppé, on the other hand, was defined by the presence of horseshoe and usually also flat dissepiments in a narrow dissepimentarium, with an epitheca surrounding individual corallites. All the genera included in this family by Schouppé, with the exception of *Synaptophyllum*, belong to the Phillipsastraeidae as defined herein.

Różkowska (1957 : 82) rejected her earlier classification in favour of that proposed by Soshkina (1949) to the extent of placing all horseshoe dissepimentate genera in the Thamnophyllidae. Różkowska referred to Schouppé's (1956 : 151) views but decided to separate those forms with horseshoe dissepiments from those without among the group with trabecular fans. Różkowska (1965 : 261), however, accepted almost completely Schouppé's (1958) classification and erected a new family, the Marisastridae, for Phillipsastraeacea with an epitheca but no horseshoe dissepiments (see Scrutton 1967).

On the other hand, Strusz (1965) rejected Schouppé's (1958) familial and ordinal groupings, placing all genera with horseshoe dissepiments in the Phacellophyllidae. Genera with trabecular fans but no horseshoe dissepiments he included in the Disphyllidae. Strusz (1965 : 523) drew attention to a distinction between forms with " half fans " and full " disphylloid fans " within this family but placed no particular taxonomic significance upon it.

The confused classification of this group of corals reflects the difficulty of distinguishing clear phylogenetic relationships between the genera involved. Morphology is extremely variable, particularly in massive forms, and results in general gradations between the characters considered diagnostic of different family and subfamily groups. A particular feature of more recent classifications resulting from this is the uncertainty in placing corals lacking horseshoe dissepiments but having a fan shaped arrangement of the septal trabeculae. Schouppé (1958) grouped them with the horseshoe bearing forms whilst Strusz (1965) grouped them with the disphyllids *sensu stricto*. All workers are agreed, however, that horseshoe dissepiments and the related trabecular fans must be considered of particular importance in taxonomy. Horseshoe dissepiments are unique to this group of Devonian corals and great stress has been laid, particularly by Soshkina (1949), Schouppé (1956) and Różkowska (1957) on the development of a pseudohexacoralloid trabecular pattern.

The trabecular arrangement alone, however, has, in the writer's opinion, been somewhat overstressed and does not justify the rank of suborder *sensu* Schouppé (1958). On the other hand, the development of specialized dissepimental types (horseshoe and peneckielloid dissepiments), with their related trabecular structure, defines with relative clarity a group of corals whose general morphological characteristics support a close family relationship. This group includes the genus *Phillipsastrea* (as defined herein) and should be classified as the Phillipsastraeidae. The writer does not agree with Strusz (1965 : 524) concerning the use of this family name. It must be noted that the generic name *Phillipsastrea* has been used far more often in a disphyllid sense than the corresponding family name. The genus, however, should not be suppressed simply because its type species has been imperfectly known in the past and in this case, the change in concept of the family name will naturally follow that of the genus.

The genera with reflexed dissepimentaria lacking horseshoe or peneckielloid dissepiments but possessing an open fan shaped arrangement of the trabeculae form a group of their own, intermediate in character between the Phillipsastraeidae as defined herein and the disphyllids *sensu stricto*. This is formalized in the family Marisastridae *sensu* Scrutton (1967). Finally, the Disphyllidae is here restricted to forms in which the trabeculae are arranged in half fans, or in a sub-parallel sense throughout on non-reflexed dissepimentaria. This family, in the writer's opinion, should be interpreted to conform strictly to the dissepimental pattern of the type genus *Disphyllum*.

Family **PHILLIPSASTRAEIDAE** Roemer 1883

1883 Phillipsastraeidae Roemer 389.
partim 1922 Campophyllidae Wedekind 3.
partim 1929 Pexiphyllidae Walther 117.
partim 1939 Campophyllidae; Soshkina : 12.
partim 1939 Cyathophyllidae; Sanford : 408.
partim 1939 Disphyllidae Hill 224.
partim 1940 Disphyllidae; Hill : 258.
partim 1942c Disphyllidae; Hill : 186.
partim 1949 Disphyllidae; Stumm : 31.
partim 1949 Thamnophyllidae Soshkina : 76.
partim 1949 Peneckiellidae Soshkina : 141.
partim 1949 Neocolumnariidae Soshkina : 145.
partim 1950 Disphyllidae; Wang : 217.
partim 1951 Disphyllidae; Taylor : 183.

partim 1952 Disphyllidae; Lecompte : 470.
partim 1953 Disphyllidae; Różkowska : 9.
partim 1954a Phillipsastreidae; Hill : 14.
partim 1954b Phillipsastreidae; Hill : 107.
partim 1955 Columnariidae; Glinski : 86.
partim 1956 Phillipsastraeidae; Hill : 279.
1957 Thamnophyllidae; Różkowska : 83.
partim 1958 Macgeeidae; Schouppé : 218.
partim 1958 Phillipsastraeidae; Schouppé : 232.
partim 1959 Disphyllidae; Middleton : 152.
partim 1959 Phillipsastraeidae; McLaren : 22.
partim 1960 Thamnophyllidae; Spassky : 44.
partim 1961 Phillipsastraeidae; Semenoff-Tian-Chansky : 294.
1962 Thamnophyllidae; Soshkina : 308.
partim 1962 Disphyllidae; Soshkina & Dobrolubova : 334.
partim 1962 Phillipsastraeidae; Soshkina & Dobrolubova : 336.
1964 Phacellophyllidae; Pedder : 366.
1965 Phacellophyllidae; Strusz : 554.
1966 Phacellophyllidae; Pedder : 183.

Type genus. *Phillipsastrea* d'Orbigny 1849 : 12.

Diagnosis. Solitary, dendroid, phaceloid or massive rugose corals. Septa of two orders, major and minor, more or less dilated at the tabularium boundary which is usually sharply defined. Characterized by an area of divergence in the septal trabeculae centred on a complete or incomplete series of horseshoe dissepiments, peneckielloid dissepiments or a series of highly globose dissepiments occasionally modified to a horseshoe form.

Distribution. Lower and particularly Middle and Upper Devonian of Europe, Asia, Australia and North America.

Discussion. Of the genera assigned to this family, all but two have a more or less well developed series of horseshoe dissepiments. The exceptions are *Peneckiella* and *Frechastraea* gen. nov.

Peneckiella may show considerable variation in dissepimental form but is characterized by the development of peneckielloid dissepiments. Frequently these are accompanied by sigmoidal, horseshoe and flat dissepiments in varying proportions. Różkowska (1960 : 32, 48, 50) who named the *Peneckiella* dissepimental types considered them to be the breakdown products of a typical *Thamnophyllum* dissepimentarium, and that *Peneckiella* evolved from this genus.

The species and subspecies of *Frechastraea* develop rare horseshoe dissepiments against the tabularium junction. This genus is thought to have evolved from *Phillipsastrea* principally through the gradual loss of horseshoe dissepiments and thus should be classified with the Phillipsastraeidae.

The full list of genera here included in the Phillipsastraeidae is as follows:

Phillipsastrea d'Orbigny 1849 (Synonyms *Smithia*, *Pachyphyllum*, *Medusaephyllum*, ?*Streptastrea*, *Pseudoacervularia* and ?*Keriophylloides*).
Macgeea Webster 1889 (Synonyms *Pexiphyllum* and *Protomacgeea*).
Thamnophyllum Penecke 1894 (Synonym *Phacellophyllum*).
Trapezophyllum Etheridge 1899.

Peneckiella Soshkina 1939 (Synonyms *Acinophyllum* and *Sudetia*).
Sulcorphyllum Pedder 1964.
Bensonastraea Pedder 1966.
Frechastraea gen. nov. (see p. 231).

Synaptophyllum Simpson 1900 was long considered to develop horseshoe dissepiments and to belong to this group of corals. McLaren (1959), however, has shown that this genus had been wrongly used due to the misinterpretation of the type species.

The genera fall roughly into two groups. *Phillipsastrea*, *Sulcorphyllum*, *Bensonastraea* and *Frechastraea* usually have several rows of normal dissepiments as well as the modified ones, whilst *Macgeea*, *Thamnophyllum*, *Peneckiella* and *Trapezophyllum* commonly have only two series of dissepiments, one horseshoe or peneckielloid and the other usually flat. Both Schouppé (1958) and Różkowska (1965) regarded the presence (in the second group) or absence of an epitheca between corallites as an additional criterion when they advocated a division at the family level along these lines. Różkowska has particularly stressed wall structure as important in familial classification.

Unfortunately, there are several exceptions to this grouping which mitigate against even subfamily status. Species of *Phillipsastrea* are known which have an epitheca around some corallites (Scrutton 1967 : 266) whilst a topotype of *Trapezophyllum elegantulum* (B.M. (N.H.) R46001) is pseudocerioid at least in part. The number of rows of dissepiments can be very variable in some species of *Thamnophyllum* (for example *T. soshkinae* (Różkowska)) and *Frechastraea* (for example *F. goldfussi* (de Verneuil & Haime)). Further, a classification based on dissepimental rows would place *Sulcorphyllum* in a different group to *Trapezophyllum* whereas the two genera appear to be closely related. Thus it is preferred not to recognize subfamily divisions in the Phillipsastraeidae.

Genus ***PHILLIPSASTREA*** d'Orbigny 1849

1849 *Phillipsastrea* d'Orbigny : 12.
partim 1850 *Lithostrotion*; d'Orbigny : 106.
partim 1850 *Favastraea*; d'Orbigny : 107.
partim 1850 *Actinocyathus*; d'Orbigny : 107.
partim 1850 *Phillipsastraea*; d'Orbigny : 107.
1850 *Pachyphyllum* Edwards & Haime : 68.
partim 1850 *Acervularia*; Edwards & Haime : 70.
1850 *Phillipsastrea*; Edwards & Haime : 70.
1851 *Pachyphyllum*; Edwards & Haime : 168, 396.
partim 1851 *Acervularia*; Edwards & Haime : 414 (*non* 171).
partim 1851 *Smithia* Edwards & Haime : 171, 421.
partim 1851 *Syringophyllum*; Edwards & Haime : 449 (*non* 173).
1851 *Arachnophyllum*; M'Coy : 72.
1853 *Pachyphyllum*; Edwards & Haime : 234.
partim 1853 *Acervularia*; Edwards & Haime : 236.
partim 1853 *Smithia*; Edwards & Haime : 240.
1853 *Syringophyllum*; Edwards & Haime : 242.
partim 1855 *Acervularia*; F. A. Roemer : 30.

1855 *Medusaephyllum* F. A. Roemer : 33.
1855 *Smithia*; F. A. Roemer : 33.
? 1856 *Streptastrea* Sandberger & Sandberger : 416.
1881 *Pseudoacervularia* Schlüter : 84.
partim 1883 *Phillipsastraea*; C. F. Roemer : 389.
partim 1883 *Pachyphyllum*; C. F. Roemer : 392.
partim 1885 *Phillipsastrea*; Frech : 44.
1885 *Phillipsastrea* (*Pachyphyllum*); Frech : 65.
partim 1889 *Phillipsastraea*; Schafer : 398.
partim 1896 *Phillipsastrea*; Gürich : 178.
1896 *Pachyphyllum*; Gürich : 181.
1909 *Smithia*; Gürich : 102.
1917 *Phillipsastraea*; Smith : 284.
1935 *Pachyphyllum*; Lang & Smith : 554.
partim 1935 *Phillipsastraea*; Lang & Smith : 556.
partim 1939 *Phillipsastraea*; Hill : 236.
1940 *Medusaephyllum*; Lang, Smith & Thomas : 83.
1940 *Pachyphyllum*; Lang, Smith & Thomas : 92.
1940 *Phillipsastraea*; Lang, Smith & Thomas : 99.
1940 *Pseudoacervularia*; Lang, Smith & Thomas : 108.
? 1940 *Streptastraea*; Lang, Smith & Thomas : 125.
partim 1942a *Phillipsastrea*; Hill : 153.
partim 1942b *Phillipsastrea*; Hill : 186.
1942c *Phillipsastrea*; Hill : 186.
partim 1945 *Phillipsastraea*; Smith : 36.
partim 1949 *Phillipsastraea*; Stumm : 34.
1949 *Pachyphyllum*; Stumm : 37.
partim 1950 *Phillipsastraea*; Wang : 220.
1951 *Phillipsastrea*; Taylor : 192.
1951 *Pachyphyllum*; Taylor : 193.
1951 *Pachyphyllum*; Soshkina : 84.
? 1951 *Keriophylloides* Soshkina : 102.
partim 1952 *Pachyphyllum*; Soshkina : 86.
partim 1952 *Phillipsastraea*; Lecompte : 471.
1953 *Pachyphyllum*; Różkowska : 39.
1953 *Pseudoacervularia*; Rózkowska : 49.
partim 1954a *Phillipsastrea*; Hill : 14.
? 1954b *Phillipsastrea*; Hill : 107.
1954 *Pachyphyllum*; Soshkina : 68.
1956 *Pachyphyllum*; Różkowska : 317.
partim 1956 *Phillipsastrea*; Hill : 280.
1956 *Pachyphyllum*; Hill : 282.
partim 1958 *Phillipsastraea*; Schouppé : 233.
1958 *Pachyphyllum*; Bulvanker : 89.
partim 1959 *Phillipsastraea*; Middleton : 156.
1961 *Pachyphyllum*; Semenoff-Tian-Chansky : 303.
partim 1962 *Phillipsastraea*; Soshkina & Dobrolubova : 336.
1964 *Phillipsastraea*; Fontaine : 84.
1965 *Phillipsastrea*; Strusz : 564.

But not:
1819 *Acervularia* Schweigger : tab. 6.
1828 *Lithostrotion* Fleming : 508.
1846 *Arachnophyllum* Dana : 186.

1849 *Actinocyathus* d'Orbigny : 12.
1850 *Syringophyllum* Edwards & Haime : 72.
1851 *Phillipsastrea*; Edwards & Haime : 173, 447.
1852 *Phillipsastraea*; Edwards & Haime : 203.
1855 *Syringophyllum*; Edwards & Haime : 295.
1951 *Phillipsastraea*; Soshkina : 95.
1952 *Phillipsastraea*; Soshkina : 101.
1953 *Phillipsastraea*; Różkowska : 57.
1954 *Phillipsastraea*; Soshkina : 45.
1958 *Phillipsastraea*; Bulvanker : 118.
1960 *Phillipsastraea*; Spassky : 65.

DIAGNOSIS. Cerioid, pseudocerioid, astraeoid, thamnasterioid, aphroid or rarely secondarily phaceloid, rugose corals. Major and minor septa with spindle-shaped dilatation at tabularium boundary. In dissepimentarium, a series of horseshoe dissepiments is well developed at or near junction with tabularium; several series of normal dissepiments also present. Tabulae complete or incomplete.

TYPE SPECIES. (Selected by Edwards & Haime 1850 : 71). *Astrea hennahii* Lonsdale (1840 : 697, pl. 58, figs. 3, 3*b*, *non* fig. 3*a*) = *Astraea hennahii* Lonsdale; Phillips (1841 : 12, pl. 6, figs. 16αa, 16βb, 16βc, *non* pl. 7, fig. 15D): upper Givetian limestones; Barton Quarry, Torquay.

DISTRIBUTION. Middle and Upper Devonian of Europe and Asia. Lower and Middle Devonian of Australia. Upper Devonian of North America.

DISCUSSION. *Phillipsastrea* was erected by d'Orbigny (1849 : 12) who quoted as examples of the genus "*Astrea parallela* et *hennahii* Phillips". In the following year he redefined the genus (1850 : 107), spelling it this time *Phillipsastraea* and splitting up the specimens illustrated by Lonsdale (1840) and Phillips (1841) as *A. hennahi* among the genera *Phillipsastrea, Lithostrotion* and *Actinocyathus.* D'Orbigny's original spelling *Phillipsastrea* is employed here following Hill (1956 : 279) who considered the spelling *Phillipsastraea* to be a *nomen vanum.*

The confusion created by Edwards & Haime (1850 : 70; 1851 : 173) who quoted first "*Astrea hennahi* Lonsdale" and later *Erismatolithus Madreporites radiatus* Martin (1809, pl. 18) as type species of *Phillipsastrea* has been clearly documented by Smith (1917 : 284). He showed the selection of *A. hennahi* to be valid and placed *Phillipsastrea radiata* and other Carboniferous species assigned to *Phillipsastrea* in the genera *Aulina* and *Orionastraea.*

Edwards & Haime's invalid designation however was still accepted by Russian workers up to the beginning of this decade (see Soshkina 1954 : 45; Bulvanker 1958 : 118; Spassky 1960 : 65) and Soshkina (1952 : 86) described *A. hennahi* Lonsdale as a species of *Pachyphyllum.* More recently, however, Soshkina & Dobrolubova (1962 : 336) have assigned the correct type species to *Phillipsastrea.*

Various authors in the last century, particularly Edwards & Haime, assigned a number of Devonian colonial corals to *Acervularia* Schweigger. In fact, Edwards & Haime (1850 : 70) unwarrantably cite *Acervularia roemeri* de Verneuil & Haime as type species of that genus. *Acervularia,* however, the type species, by monotypy, of which is *Madrepora ananas* Linnaeus 1758 : 797 = *Acervularia baltica* Schweigger

1819, Table 6; Upper Silurian, Gotland, Sweden, is typically Silurian with only a superficial resemblance to the Devonian forms. With the closer study of internal structures in later years, the Devonian species of *Acervularia* were removed from that genus and usually reassigned to *Phillipsastrea* (see Frech 1885 : 44). Schlüter (1881 : 84) had, in fact, erected a new genus *Pseudoacervularia* expressly to cover the Devonian " acervulariids ", but this genus has been little used. Indeed, a type species was not selected until Lang, Smith & Thomas (1940 : 108) chose *Acervularia coronata* Edwards & Haime for that purpose. Unfortunately the type specimens of *A. coronata* are missing but the species is almost certainly conspecific with *Phillipsastrea hennahi*, and *Pseudoacervularia* is a subjective synonym of *Phillipsastrea*.

Różkowska (1953 : 39), apparently unaware of Lang, Smith & Thomas' selection, invalidly chose *Acervularia macrommata* F. A. Roemer as type species of *Pseudoacervularia*. She described several species of that genus, all of which should be placed in *Phillipsastrea*.

A most critical factor in the taxonomic position and interpretation of *Phillipsastrea* has been the emphasis placed by Schouppé (1958 : 156) on the development of horseshoe dissepiments in the lectotype of the type species. Hitherto, the presence of these specialized dissepiments in the lectotype had not been widely realized and the genus had been either restricted to species lacking horseshoe dissepiments (Stumm 1949 : 34; Różkowska 1953 : 57; Hill 1956 : 280), or considered to include species both with and without horseshoe dissepiments (Lang & Smith 1935 : 556; Hill 1939 : 236; Smith 1945 : 36). In addition, Edwards & Haime (1850 : 68) had erected the genus *Pachyphyllum* with *P. bouchardi* as type species. The latter has long been known to develop horseshoe dissepiments and many authors (Stumm 1949 : 37; Soshkina 1951 : 84; Różkowska 1953 : 39) have used the genus specifically for Middle and Upper Devonian massive phillipsastreids with well developed horseshoe dissepiments.

Schouppé (1958 : 233 *et seq.*), however, placed *Pachyphyllum* in synonymy with *Phillipsastrea*. At the same time, he removed all the forms previously assigned to the latter genus which he thought to lack horseshoe dissepiments and placed them in *Billingsastraea* Grabau (see comments under that genus by Scrutton (1967 : 276) and under *Frechastraea* gen. nov. herein).

The writer agrees with Schouppé's concept of *Phillipsastrea* with the exception of the placing of *Haplothecia* Frech. Schouppé (1958 : 201) claimed that the type species of the latter developed horseshoe dissepiments. However, an examination of the lectotype of *H. filata* (Schlotheim), type species of *Haplothecia*, does not substantiate this (Scrutton 1967 : 271) and the genus is here regarded as quite distinct from *Phillipsastrea*.

Semenoff-Tian-Chansky (1961 : 303) was not convinced that *Phillipsastrea* and *Pachyphyllum* should be considered congeneric and he mentioned two particular points of apparent difference in overall size and dissepimental arrangement. With regard to the considerable disparity in size between the respective type species, the existence of species of intermediate size must not be overlooked—for example *Phillipsastrea ananas* (Goldfuss), *P. devoniensis* (Edwards & Haime), *P. ibergensis* (F. A. Roemer) and *P. chenouensis* (Semenoff-Tian-Chansky). In fact it would appear that, quite fortuitously, *Phillipsastrea hennahi* is one of the smallest and *Pachyphyllum bouchardi* the largest of the species assigned to *Phillipsastrea*. The apparent discrepancy between *Pachyphyllum* and *Phillipsastrea* in the arrangement of the normal dissepiments was based on a comparison with Schouppé's (1958, text-fig. 21; pl. 5, fig. 1) longitudinal illustrations of *P. hennahi*. As remarked elsewhere, although purporting to come from the lectotype, they are completely different from longitudinal slides, and peels taken from that specimen by the writer, which are illustrated here (Pl. 1, figs. 2–4, 6). There is in fact no basic difference in the dissepimental arrangement between *P. hennahi* and *P. bouchardi*.

Phillipsastrea is thus interpreted as including all those Devonian massive corals, excepting species of *Trapezophyllum*, *Sulcorphyllum* and *Bensonastraea*, in which a series of horseshoe dissepiments is well developed in the dissepimentarium. *Trapezophyllum* Etheridge (1899 : 32) differs from *Phillipsastrea* in possessing only one row of flat dissepiments peripheral to the horseshoe series and in this respect is related more closely to *Thamnophyllum*. *Sulcorphyllum* Pedder (1964 : 366) is like *Trapezophyllum* but with several rows of normal dissepiments separating the peripheral flat dissepiments from the horseshoes adjacent to the tabularium. The irregular, incomplete tabulae of this genus are unlike those found in European phillipsastreids. *Sulcorphyllum* is, for the present, considered distinct from *Phillipsastrea* but a better knowledge of the variation in the former may require its taxonomic position to be reconsidered in the future. *Bensonastraea* Pedder (1966 : 183) is distinguished by its vepreculate and peripherally degenerate septa, and complex dissepimentarium.

Phillipsastrea hennahi hennahi (Lonsdale)

Plate 1, figs. 1–6; Plate 2, figs. 1–4

1840 *Astrea* (*Siderastrea*) *hennahii* Lonsdale : 697 *pars*, pl. 58, figs. 3, 3*b* (*non* 3*a*).
1841 *Astraea hennahii* Lonsdale; Phillips : 12 *pars*, pl. 6, figs. 16αa, 16βb, 16βc (*non* pl. 7, fig. 15D).
1841 *Astraea intercellulosa* Phillips : 12, pl. 6, fig. 17.
? 1843 *Astraea hennahii* Lonsdale; F. A. Roemer : 5, pl. 2, fig. 13.
1849 *Phillipsastrea hennahii* (Phillips) d'Orbigny : 12 *pars*.
1850 *Lithostrotion hennahii* (Lonsdale) d'Orbigny : 106.
1850 *Favastraea intercellulosa* (Phillips) d'Orbigny : 107.
1850 *Actinocyathus hennahii* (Phillips) d'Orbigny : 107.
1850 *Phillipsastraea hennahii* (Phillips); d'Orbigny : 107 *pars*.
? 1850 *Acervularia roemeri* de Verneuil & Haime : 162.
1850 *Phillipsastrea cantabrica* de Verneuil & Haime : 162 (*nomen nudum*).
1850 *Phillipsastrea hennahi* (Lonsdale); Edwards & Haime : 71 *pars*.
1851 *Acervularia coronata* Edwards & Haime : 416.
? 1851 *Acervularia roemeri* de Verneuil & Haime; Edwards & Haime : 420.
1851 *Smithia hennahii* (Lonsdale) Edwards & Haime : 421.
1851 *Syringophyllum? cantabricum* (de Verneuil & Haime) Edwards & Haime : 451.
1851 *Arachnophyllum hennahi* (Lonsdale) M'Coy: 72.
1853 *Acervularia coronata* Edwards & Haime; Edwards & Haime: 237, pl. 53, figs. 4a–b (?fig. 4).
1853 *Acervularia roemeri* de Verneuil & Haime; Edwards & Haime : 239, pl. 54, figs. 3, 3*a*.
1853 *Smithia hennahii* (Lonsdale); Edwards & Haime : 240, pl. 54, figs. 4–4*d*.

1853 *Syringophyllum cantabricum* (de Verneuil & Haime); Edwards & Haime : 242, pl. 55, figs. 3–3*a*.
? 1855 *Smithia hennahi* (Phillips); F. A. Roemer : 33, pl. 6, fig. 25.
? 1856 *Streptastrea longiradiata* Sandberger & Sandberger : 416, pl. 37, figs. 3–3*b*.
? 1879 *Acervularia roemeri* de Verneuil & Haime; Quenstedt : 535, pl. 162, fig. 38.
1879 *Astrea hennahii* Lonsdale; Quenstedt : 535.
1883 *Acervularia coronata* Edwards & Haime; C. F. Roemer : 352.
? 1883 *Acervularia roemeri* de Verneuil & Haime; C. F. Roemer : 353.
1883 *Phillipsastraea hennahii* (Lonsdale); C. F. Roemer : 390.
1885 *Phillipsastrea roemeri* (de Verneuil & Haime) Frech : 57 *pars*, pl. 4, ? fig. 2 (*non* figs. 1, 3–5).
1885 *Phillipsastrea hennahi* (Lonsdale); Frech : 59 *pars*, pl. 5, fig. 1, (*non* figs. 2–4).
1917 *Phillipsastraea hennahi* (Lonsdale); Smith : 284, pl. 22, figs. 1–4.
1945 *Phillipsastraea hennahi* (Lonsdale); Smith : 37, pl. 19, figs. 1*a*, *b*.
1952 *Pachyphyllum hennahi* (Lonsdale) Soshkina : 86.
1958 *Phillipsastraea hennahi* (Lonsdale); Schouppé : 235, ?text-figs. 20, 21, ?pl. 5, fig. 1.
1959 *Phillipsastraea hennahi* (Lonsdale); Middleton : 156.
1963 *Phillipsastraea hennahi* (Lonsdale); Fontaine : 84, pl. 8, figs. 5, 6.

But not:
1953 *Pseudoacervularia roemeri* (de Verneuil & Haime) Różkowska: 53, text-figs. 27, 28, pl. 7, figs. 3, 4.

DIAGNOSIS. Astraeoid tending to thamnasterioid *Phillipsastrea*. Mean tabularium diameter 2·45 mm. with 10 to 16 major septa (topotype sample). Septa thin peripherally, with a variable spindle-shaped thickening at tabularium junction. Dissepimentarium composed of several rows of normal dissepiments with a single series of horseshoe dissepiments developed against tabularium. Tabulae complete or incomplete, usually in form of wide flat plates with downturned edges. Increase lateral.

LECTOTYPE. Selected by Edwards & Haime (1851 : 421). The original of Lonsdale's (1840, pl. 58) figures 3 and 3*b* which is GSM (Geol. Soc. Coll.) 6185; upper Givetian limestones; Barton Quarry, Torquay.

MATERIAL. Barton Quarry: OUM D514 (Colony 1), OUM D306 (Colony 2), OUM D512 (Colony 3), BM(NH) R5615 (Colony 4). Other measured specimens: GSM (Geol. Soc. Coll.) 6185 (lectotype), OUM D515–6, OUM D518–20, OUM D522, TM(JB) 107–8, TM(JB) 120. Additional material: OUM D240 (= D282), OUM D513, OUM D517, OUM D523, TM(JB) 139.

Lummaton Quarry: TM(JB) 61 (Colony 1), TM(JB) 59 (Colony 2), BM(NH) R23484 (Colony 3). Other measured specimens: TM(JB) 63–4, TM(JB) 78–9. Additional material: TM(JB) 62, TM(JB) 69.

Wolborough Quarry: OUM D521.

Babbacombe Cliff: BM(NH) R46176.

Dartington Hall: GVM13/1, GVM14/2.

Torquay, South Devon: OUM D74 (holotype, *Astraea intercellulosa* Phillips), GSM (Geol. Soc. Coll.) 6189 (lectotype here chosen, *Syringophyllum cantabricum* Edwards & Haime).

Distribution. England: upper Givetian limestones of Barton and Lummaton quarries, Torquay; middle Givetian limestones of Wolborough Quarry, Newton Abbot; Givetian limestones, 100 ft. above sea level, south end Babbacombe cliffs, Torquay; middle Givetian limestones of Dartington Hall area (Middleton 1959); Middle Devonian, Plymouth (Phillips 1841). Devonian, Kikai, Yunnan (Fontaine 1963). Also represented in the Frasnian, Ibergerkalk, Bad Grund, Harz, Germany (Frech 1885). Middle Devonian, Pola de Gordon, Léon, Spain (de Verneuil & Haime 1850).

Description. All specimens are incomplete and details of the colony exterior, its overall size and shape are unknown. The largest specimen examined was, when complete, 17 × 14 cm. in surface area and 5 cm. deep (it is now in two pieces numbered separately as OUM D240 and OUM D282).

Colonies are astraeoid tending to thamnasterioid, with a straight or zigzagged pseudotheca of variable strength separating the corallites. This pseudotheca may break down round parts of the corallite margins when the septa run more or less confluently from one corallite to the next.

The septa, major and minor, are very thin peripherally, less than 0·1 mm. and normally about 0·025 mm. in thickness. They may have smooth or slightly roughened sides and rarely some separation of the trabeculae but they are never truly carinate. They are usually sinuous, seldom straight, in the dissepimentarium and occasionally curved in a constant direction to form a vortex. The septa develop a spindle-shaped dilatation in the region of the tabularium junction. It is extremely variable both within colonies and individual corallites, ranging normally between 0·15 and 0·25 mm. width and 1 to 2 mm. length (see, for example TM(JB)79, Pl. 2, fig. 1).

Within the tabularium, the major septa usually taper smoothly and end somewhat short of the axis of the corallite. Occasionally, however, some may reach the axis, or cross the tabularium periaxially to join with major septa in the adjacent quadrant of the corallite. Rarely the axial ends of the major septa may develop slight lobate thickenings. The minor septa do not enter the tabularium.

Dissepiments are usually uniserial but may occasionally be multiserial between adjacent septa. In cross-section they are well spaced peripherally, becoming more crowded towards the tabularium junction which is sharply defined. Against this junction, the trace of a single series of horseshoe dissepiments is sometimes clearly seen (Pl. 2, fig. 2 corallite in right centre).

In longitudinal-section, the dissepimentarium is composed of several rows of small, normal dissepiments, between 0·2 and 0·5 mm. in height. They are weakly arched peripherally but become increasingly globose towards the tabularium boundary. The dissepiments immediately adjacent to the tabularium are modified into horseshoe form resulting in a single vertical series of more or less well developed horseshoe dissepiments (Pl. 1, figs. 2–6). The surface of the dissepimentarium slopes downwards away from this series and flattens out peripherally.

The tabulae are complete or incomplete, more usually the latter. In general they are strikingly flat and parallel across the axis of the tabularium, usually with down-turned peripheral edges. There is a limited development of vesicular, periaxial

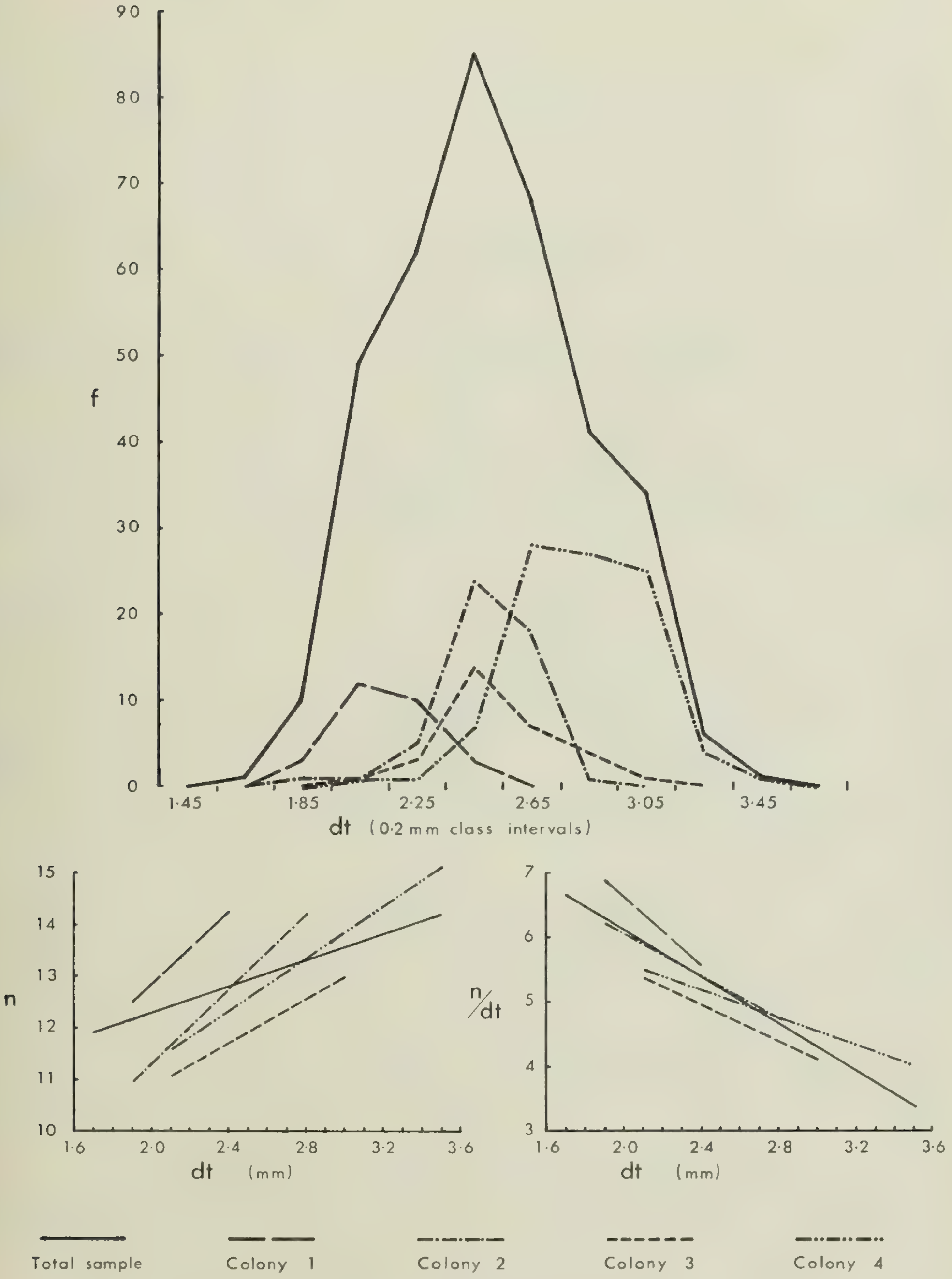


FIG. 9. *Phillipsastrea hennahi hennahi* (Barton sample).

TABLE 4.*a*. Statistical data for some characters of *Phillipsastrea hennahi hennahi* (Barton sample). *b*. Statistical data forsome characters of *Phillipsastrea hennahi hennahi* (Lummaton sample).

		(*a*)					(*b*)			
		Total sample	Colony 1	Colony 2	Colony 3	Colony 4	Total sample	Colony 1	Colony 2	Colony 3
	N	357 (14)	28	50	30	94	261 (7)	71	51	54
	O.R.	1·7–3·5	1·9–2·4	1·9–2·8	2·1–3·0	2·1–3·5	1·7–3·0	1·7–2·8	2·0–2·9	2·1–2·7
	$\bar{\mathbf{x}}$	2·45	2·14	2·49	2·55	2·82	2·32	2·31	2·40	2·43
dt	**s**	0·33	0·16	0·17	0·21	0·23	0·24	0·24	0·17	0·12
	C.V.	13·27	7·23	6·75	8·09	8·07	10·13	10·58	6·95	5·05
	$\mathbf{S.E._m}$	0·018	0·029	0·024	0·038	0·024	0·015	0·029	0·023	0·17
	O.R.	10–16	12–14	12–15	11–13	11–15	10–15	10–14	11–14	10–14
	$\bar{\mathbf{x}}$	12·92	13·36	13·08	12·03	13·40	12·67	12·34	12·57	12·39
n	**s**	0·42	0·55	0·60	0·43	0·57	0·37	0·41	0·41	0·55
	C.V.	3·22	4·08	4·61	3·61	4·21	2·89	3·34	3·27	4·46
	$\mathbf{S.E._m}$	0·022	0·10	0·085	0·079	0·058	0·023	0·049	0·058	0·075
	O.R.	3·79–7·37	5·42–7·00	4·62–6·32	4·14–5·72	3·93–5·72	4·23–7·78	4·23–7·37	4·44–6·50	4·58–6·08
	$\bar{\mathbf{x}}$	5·25	6·28	5·26	4·74	4·77	5·52	5·40	5·26	5·09
n/dt	**s**	0·61	0·41	0·28	0·29	0·24	0·45	0·50	0·28	0·12
	C.V.	11·69	6·47	5·30	6·16	4·94	8·16	9·29	5·29	2·39
	$\mathbf{S.E._m}$	0·033	0·077	0·039	0·053	0·024	0·028	0·060	0·039	0·017
Graphs:—										
	r	0·70	0·42	0·73	0·75	0·89	0·88	0·70	0·69	0·89
n/dt	**a**	1·26	3·53	3·59	2·10	2·48	1·56	1·69	2·46	4·49
	b	9·78	5·83	4·14	6·67	6·41	9·07	8·44	6·66	1·46
n/dt /	**r**	−0·96	−0·83	−0·75	−0·89	−0·91	−0·98	−0·95	−0·88	−0·45
	a	−1·85	−2·63	−1·65	−1·41	−1·03	−1·92	−2·06	−1·67	−0·99
/**dt**	**b**	9·87	11·90	9·38	8·35	7·69	9·96	10·14	9·26	7·50

	A	At	At/A	Graph:—At/A			A	At	At/A	Graph:—At/A	
O.R.	0·86–1·54	0·034–0·065	0·035–0·074			**O.R.**	0·68–1·35	0·032–0·047	0·034–0·053		
$\bar{\mathbf{x}}$	1·08	0·046	0·045	**r**	0·78	$\bar{\mathbf{x}}$	1·01	0·041	0·042	**r**	0·69
s	0·20	0·011	0·010	**a**	0·055	**s**	0·25	0·0061	0·0072	**a**	0·024
C.V.	18·70	23·84	23·41	**b**	−0·013	**C.V.**	24·94	14·94	17·31	**b**	0·016
$\mathbf{S.E._m}$	0·054	0·0030	0·0028			$\mathbf{S.E._m}$	0·095	0·0023	0·0027		

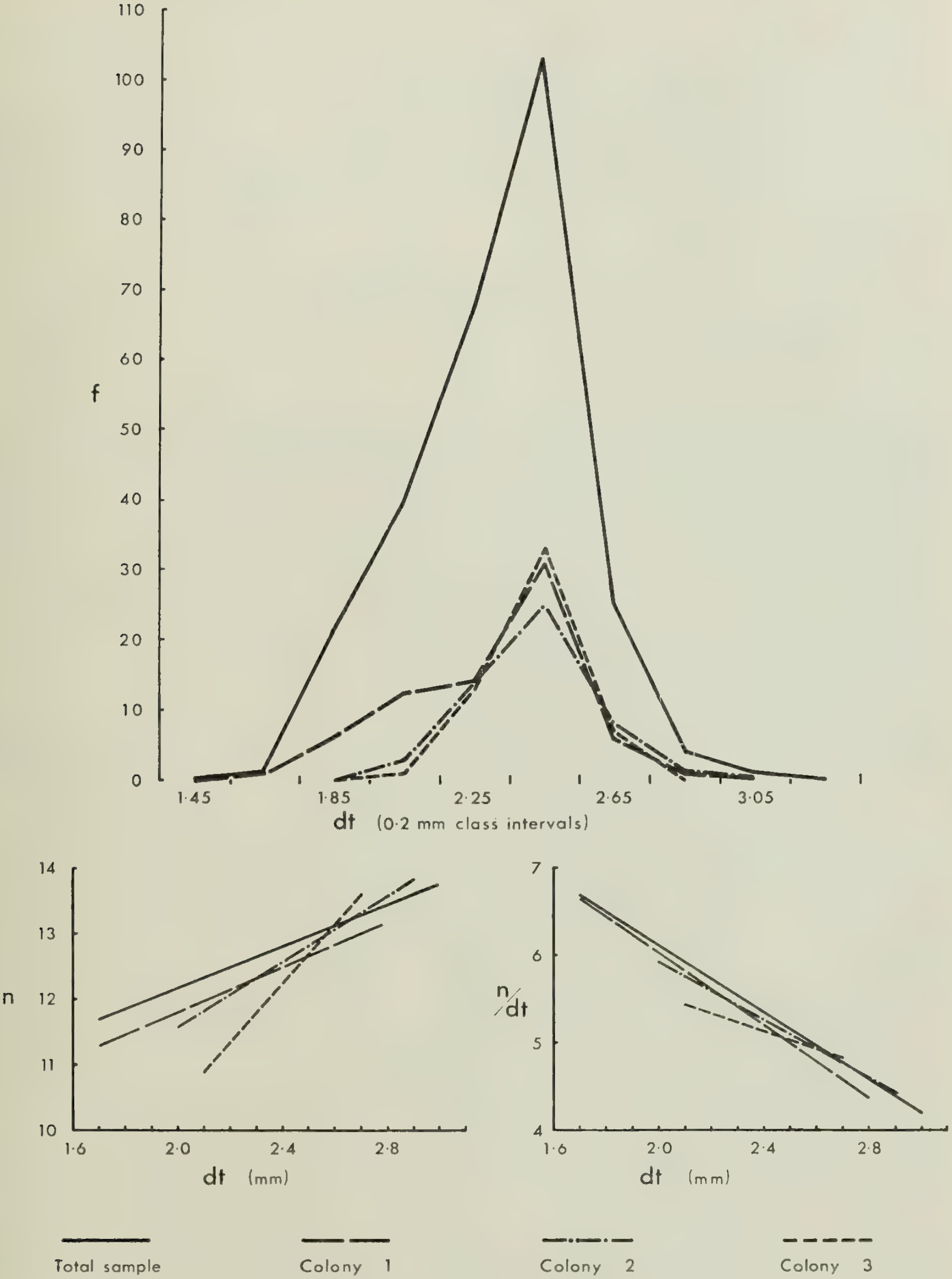


FIG. 10. *Phillipsastrea hennahi hennahi* (Lummaton sample).

elements. Tabularium structure varies in complexity from the simple, interleaved tabulae of TM(JB) 79 (Pl. 1, fig. 5) to the close spaced series of flat-topped domes in GSM (Geol. Soc. Coll.) 6185 (Pl. 1, figs. 2–4, 6).

Despite the large number of specimens examined, only one instance of lateral increase has been seen and that is in the lectotype.

Statistical analyses have been made of samples of this subspecies from the type locality, Barton Quarry (14 colonies) and Lummaton Quarry (7 colonies), both in Torquay. Four colonies from Barton and three from Lummaton have been analysed individually. The statistics are given in Table 4 and illustrated graphically in Text-figs. 9, 10 and 12.

The topotypes are characterized by a mean tabularium diameter of 2·45 mm. with 10 to 16 major septa and a mean septal-tabularium ratio of 5·25. The Lummaton specimens differ principally in having a smaller overall range and mean **dt**, and a somewhat larger mean **n/dt**.

Colonial variation at the two localities displays an interesting contrast. Generally there is a greater range in the mean values of the quantitative characters between the colonies from Barton, although variation within each colony is much the same. The Lummaton colonies, on the other hand, have very similar mean values but markedly different degrees of variation from colony to colony.

Discussion. The specimen on which Phillips (1841 : 12) erected *Astraea intercellulosa* is OUM D74 (Pl. 2, figs. 2, 3). Phillips himself had great doubts as to whether or not his specimen was distinct from Lonsdale's species. In the writer's opinion it is an atypical representative of *P. hennahi hennahi* in which the septa are virtually unthickened.

F. A. Roemer (1843 : 5, pl. 2, fig. 13) described and figured as *Astraea hennahi* Lonsdale a specimen which was later selected by de Verneuil & Haime (1850 : 162) as the type of a new species *Acervularia roemeri*. The identity of Roemer's original is uncertain but Edwards & Haime (1853 : 239, pl. 54, figs. 3, 3*a*) later recorded *A. roemeri* from Torquay. The latter's specimen, judging from their figures, is almost certainly consubspecific with *P. hennahi hennahi*. Frech (1885, pl. 4, figs. 1–5) also figured *Phillipsastrea roemeri* (de Verneuil & Haime), of which, if his interpretation was correct, the original of his fig. 2 is a topotype. Again it appears from the illustration that the specimen may be consubspecific with *Phillipsastrea hennahi hennahi*.

Edwards & Haime (1853) described and figured two species, *Acervularia coronata* and *Syringophyllum cantabricum*, previously erected by them in 1851 (p. 416 and p. 451 respectively). In the case of *A. coronata*, Edwards & Haime's original material has been lost or mislaid. From their illustrations (1853, pl. 53, figs. 4*a*, *b*) of a specimen from Barton, however, the species is almost certainly the same as the present subspecies. "*Phillipsastrea cantabrica* n. sp." in de Verneuil & Haime (1850 : 162) is a *nomen nudum* as they give neither description nor figures of the species. Edward & Haime (1851 : 451) must therefore be regarded as the authors of the species with their description of "*Syringophyllum? cantabricum* (de Verneuil & Haime)". The original of Edwards & Haime's (1853, pl. 55, figs. 3, 3*a*) figures of *Syringophyllum cantabricum* is specimen GSM (Geol. Soc. Coll.) 6189, which is here chosen as lectotype of the species (Pl. 2, fig. 4). This specimen is consubspecific with *P. hennahi hennahi.*

Schouppé (1958, text-fig. 21, pl. 5, fig. 1) published two illustrations which he stated were taken from a longitudinal peel of specimen GSM (Geol. Soc. Coll.) 6185. The structure of both the tabularium and the dissepimentarium in Schouppé's figures, however, is not that seen in this specimen although the presence of horseshoe dissepiments can be confirmed. The source of Schouppé's figures must thus be considered somewhat enigmatic.

Phillipsastrea hennahi ussheri subsp. nov.

Plate 3, figs. 1–3

Derivation of name. The subspecies is named after W. A. E. Ussher (1849–1920).

Diagnosis. Astraeoid tending to thamnasterioid *Phillipsastrea.* Mean tabularium diameter 2·04 mm. with 10 to 14 major septa (topotype sample). Septa thin peripherally but usually strongly dilated at tabularium junction, becoming laterally contiguous and forming a dense inner wall. Horseshoe dissepiments developed in a series adjacent to tabularium with several rows of normal dissepiments peripherally. Tabulae usually incomplete with narrow axial series of flat topped domes irregularly developed. Increase lateral.

Holotype. OUM D544. Lower Frasnian limestones; road cutting, 20 yd. west of the entrance to Ramsleigh Quarry, East Ogwell, near Newton Abbot.

Material. Ramsleigh Quarry: BM(NH) R23402 (Colony 1), BM(NH) R5616 (Colony 2), BM(NH) R23209 (Colony 3).

Road cutting, 40 yd. west of Ramsleigh Quarry entrance. Measured specimens: OUM D533–4.

Road cutting, 20 yd. west of Ramsleigh Quarry entrance. OUM D545.

Distribution. Lower Frasnian limestones in and around Ramsleigh Quarry.

Description. Only incomplete colonies have been found and the overall colony shape, size and external features are unknown.

The colonies are astraeoid tending to thamnasterioid with considerable variation in the strength of the pseudotheca. Perfectly confluent septa between adjacent corallites, however, are rare. Septa are thin peripherally, usually about 0·06 mm. thick, occasionally straight but more usually sinuous. The sides of the septa may be smooth or slightly crenulate; carinae are not developed. Immediately adjacent to the tabularium, the septa are dilated. The short, spindle-shaped thickening is greater on the major septa when it is usually 0·5 to 0·7 mm. long and about 0·25 mm. wide. The dilatation is a very constant feature, frequently bringing adjacent septa into contact to form a dense wall, about 0·5 mm. wide, round the tabularium. Minor septa end at the tabularium junction but the major septa thin abruptly and continue as very fine filaments, about 0·02 mm. thick, towards the axis of the corallite. Sometimes the ends of the major septa, slightly withdrawn from the axis, bear small lobate thickenings which through lateral contact may form a pseudoaulos. In

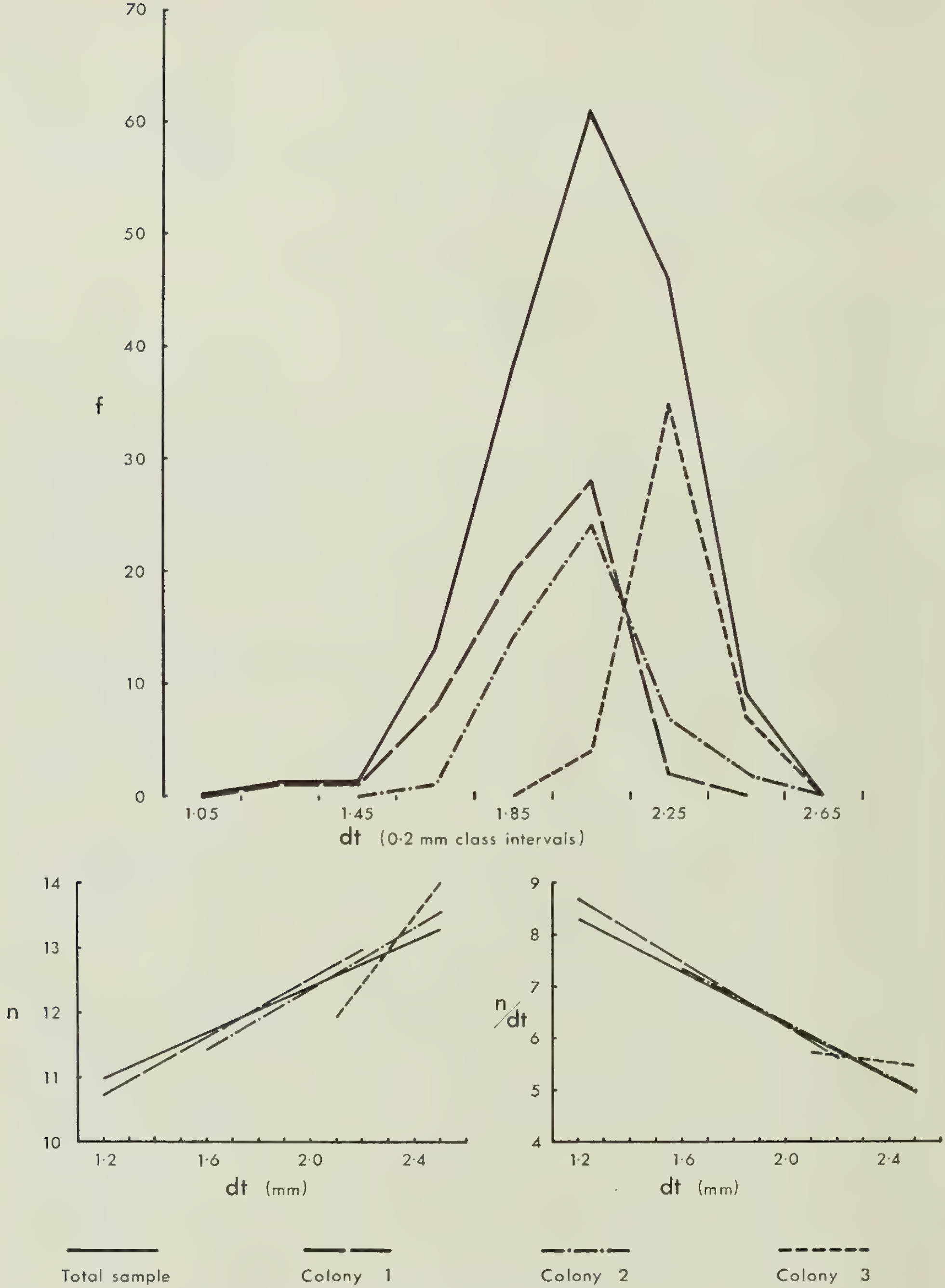


FIG. 11. *Phillipsastrea hennahi ussheri.*

TABLE 5.—Statistical data for some characters of *Phillipsastrea hennahi ussheri.*

		Total sample	Colony 1	Colony 2	Colony 3
	N	169 (5)	60	48	46
dt	**O.R.**	1·2–2·5	1·2–2·2	1·6–2·5	2·1–2·5
	$\bar{x}$	2·04	1·91	2·03	2·27
	s	0·22	0·18	0·16	0·094
	C.V.	10·61	9·47	8·01	4·14
	S.E.$_m$	0·017	0·023	0·024	0·014
n	**O.R.**	10–14	10–14	11–14	11–14
	$\bar{x}$	12·46	12·37	12·50	12·78
	s	0·38	0·39	0·37	0·48
	C.V.	3·07	3·17	2·97	3·79
	S.E.$_m$	0·029	0·051	0·054	0·071
n/dt	**O.R.**	4·76–9·16	5·71–9·16	5·20–8·12	5·00–6·19
	$\bar{x}$	6·16	6·55	6·18	5·63
	s	0·55	0·55	0·41	0·052
	C.V.	8·97	8·37	6·62	0·92
	S.E.$_m$	0·043	0·071	0·059	0·0077
Graphs:—					
n/dt	**r**	0·93	0·92	0·72	0·98
	a	1·77	2·17	2·28	5·15
	b	8·86	8·23	7·86	1·09
n/dt / dt	**r**	−0·96	−0·96	−0·91	−0·46
	a	−2·56	−3·04	−2·52	−0·55
	b	11·38	12·33	11·30	6·89

	A	**At**	**At/A**	Graph:—**At/A**	
O.R.	0·36–0·89	0·026–0·041	0·037–0·081	**r**	0·32
$\bar{x}$	0·55	0·032	0·063	**a**	0·027
s	0·21	0·0055	0·017	**b**	0·018
C.V.	37·69	17·09	26·12		
S.E.$_m$	0·092	0·0025	0·0061		

other cases, the septal ends are free, or fused in groups of two or three in the centre of the tabularium.

Usually the dissepiments are uniserial between adjacent septa and appear rather closely spaced in cross-section. Around the tabularium, and coincidental with the septal thickening, the traces of a single series of horseshoe dissepiments form two strong concentric walls (Pl. 3, fig. 1), or delimit the width of the single thick wall when the septa are in lateral contact (Pl. 3, fig. 3).

In longitudinal-section, the dissepimentarium is composed of several rows of small, globose dissepiments, usually between 0·1 and 0·3 mm. in height. Immediately adjacent to the tabularium, the dissepiments are quite sharply modified into a vertical series of horseshoes, predominantly uniserial and quite regularly developed. The surface of the dissepimentarium slopes steeply away from the series of horseshoe dissepiments but is flat over most of its area. The tabularium junction is sharply defined.

Tabularium structure is not perfectly clear from the present material. The tabulae appear to be closely spaced and usually incomplete. Often there is a wide peripheral series of horizontal plates, slightly distally concave, abutting against a central series of small, flat-topped or occasionally globular domes, which occupy a third to a quarter of the tabularium diameter. In other portions of the tabularium, this axial structure is missing and the whole width is occupied by flat, interleaved plates.

Four examples of lateral increase have been seen in BM (NH) R5616 although in each case the new individuals are well advanced.

A small sample of five colonies of this subspecies has been statistically analysed. Three of the colonies have also been treated separately to investigate colonial variation. The resulting statistics are given in Table 5 and the data illustrated graphically in Text-figs. 11 and 12.

DISCUSSION. It is possible that some of the material from Upper Devonian localities in continental Europe which has been described as *Phillipsastrea hennahi* properly belongs to this subspecies; for example, the specimen figured by Frech (1885, pl. 5, fig. 2) from the Frasnian Ibergerkalk at Bad Grund, Germany.

Comparison of the subspecies of Phillipsastrea hennahi. The main quantitative characteristics of *P. hennahi hennahi* (Barton Quarry sample) and *P. hennahi ussheri* have been statistically compared and the results are tabulated below:

dt	t = 14·69 (524° freedom)	$P \ll 0{\cdot}01$
n/dt	z (slope) = 7·38	$P \ll 0{\cdot}01$
At/A	z (slope) = 1·91	$P > 0{\cdot}01$
	z (position) = 7·02	$P \ll 0{\cdot}01$

The mean tabularium diameter for *P. hennahi ussheri* (2·04 mm.) is significantly smaller than that for *P. hennahi hennahi* (2·45 mm.). There is also a significant difference between the slopes of the correlation lines on the graph plotting **n** against **dt** for the two subspecies. The number of major septa increases slightly faster with increasing tabularium diameter in the Frasnian subspecies. The number of points on the graph plotting **At** against **A** is rather low to allow the results of a "**z**" test to be uncritically accepted (Imbrie 1956 : 237, footnote 1). Nevertheless, the significant difference in position reflects the small degree of overlap of the points for the two subspecies.

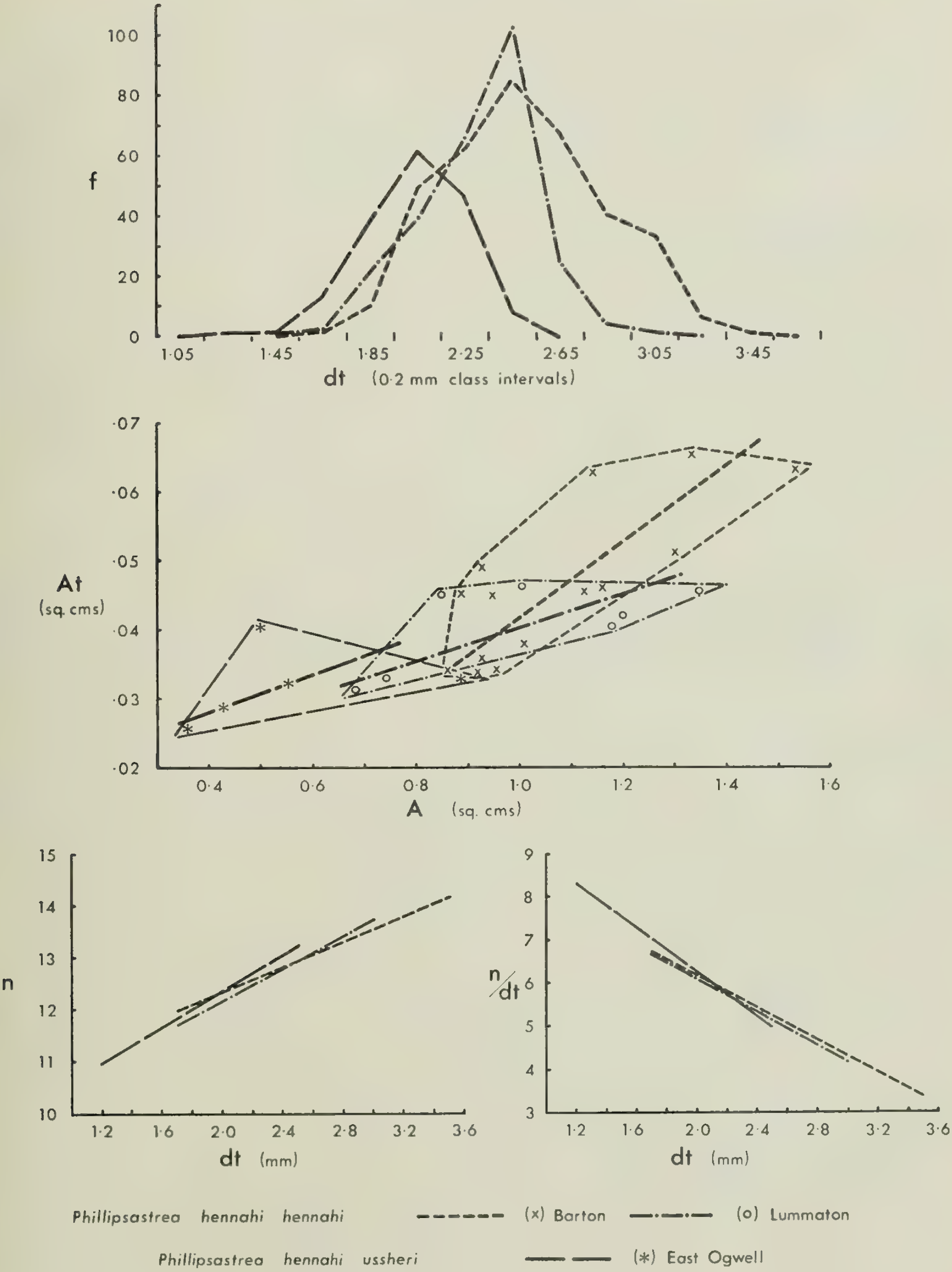


FIG. 12. Graphical comparison of some quantitative characters for the subspecies of *Phillipsastrea hennahi.*

Qualitatively the two subspecies are very similar and obviously closely related. The strong cross-sectional traces of horseshoe dissepiments, usually infilled by close packed septal tissue, which surrounds the tabularium in *P. hennahi ussheri* is, however, very distinctive. The horseshoe traces are rarely so clearly seen in *P. hennahi hennahi* and excessive septal dilatation is similarly uncommon. The major septa within the tabularium are also contrasted in the two subspecies. The abrupt attenuation of the septa, which closely approach the axis, often with a lobate thickening of their axial ends, is characteristic of *P. hennahi ussheri*. The major septa of *P. hennahi hennahi* are usually somewhat withdrawn from the axis and taper away from the dilated zone.

In longitudinal-section, the most noticeable difference between the two subspecies is in the tabularium structure. The narrow axial domes and wide, flat peripheral plates of *P. hennahi ussheri* contrast with the broad based, flat-topped domes of *P. hennahi hennahi*. There is, however, no characteristic difference between the dissepimentaria of the two subspecies.

Phillipsastrea devoniensis (Edwards & Haime)

Plate 4, figs. 1–4

1851 *Pachyphyllum devoniense* Edwards & Haime : 397.
1853 *Pachyphyllum devoniense* Edwards & Haime; Edwards & Haime : 234, pl. 52, figs. 5, 5*a*.
1883 *Pachyphyllum devoniense* Edwards & Haime; C. F. Roemer : 393, text-fig. 93.
1885 *Phillipsastrea* (*Pachyphyllum*) *devoniense* (Edwards & Haime) Frech : 67, pl. 6, figs. 2, 2*a*.
1952 *Pachyphyllum devoniense* Edwards & Haime; Soshkina : 86.

But not:
1958 *Pachyphyllum devoniense* Edwards & Haime; Bulvanker : 93, pl. 45, figs. 1*a*, *b*.

Diagnosis. Astraeoid tending to thamnasterioid *Phillipsastrea* with poorly defined corallite margins. Mean tabularium diameter 3·72 mm. with 16 to 23 major septa (South Devon sample). Septa generally thin, with slight, elongate dilatation surrounding tabularium. In longitudinal-section, a series of horseshoe dissepiments is developed just outside tabularium junction. Tabulae wide, flat, complete or incomplete.

Holotype. The original of Edwards & Haime's (1853, pl. 52) fig. 5 and 5*a*; Devonian, Torquay. This specimen is either mislaid or lost.

Material. " Rocky Valley ". Measured specimens: OUM D277, BM(NH) 74489.

?Lummaton Quarry. Measured specimen: TM(JB) 105.

Torquay, S. Devon: BM(NH) R1456.

Distribution. England: *in situ* only from middle Givetian limestones, Wolborough Quarry, Newton Abbot and ?from upper Givetian limestones, Lummaton Quarry, Torquay. Other specimens are beach pebbles, several being known from " Rocky Valley " (? = Valley of Rocks, Watcombe, north of Torquay). Also recorded from the Ibergerkalk, Bad Grund, Germany; Frasnian.

Description. Nothing is known of the overall size, shape and external features of this species.

Colonies are astraeoid tending to thamnasterioid. The septa are usually outwardly geniculate and irregularly abutting. Occasionally they may be perfectly confluent from one corallite to the next or rarely they end in the dissepimentarium with a free peripheral end. The margins of the corallites are indistinctly defined in the absence of a well formed pseudotheca.

The septa, major and minor, are 0·1 mm. or less in thickness in the dissepimentarium where they follow a straight or sinuous course. In a zone surrounding the tabularium of 1 to 1·5 mm. width, the septa have a slight, elongate dilatation, usually to about 0·2 or 0·3 mm. thickness. Minor septa project just within the tabularium. The major septa continue in a strongly attenuate form more or less to the axis, where their ends may be free and infrequently slightly thickened, or confluent with septa in the adjacent quadrant of the tabularium. Carinae are not developed.

Dissepiments are usually uniserial between adjacent septa. Just outside the tabularium, in the zone of septal dilatation, cross-sectional traces of horseshoe dissepiments are often clearly visible. The tabularium junction is clearly defined.

In longitudinal-section, the dissepimentarium is composed of several series of arched dissepiments usually between 0·2 and 0·4 mm. high. Just outside the tabularium, a slightly discontinuous single series of irregularly sized horseshoe dissepiments is developed. From the crest of the series, the dissepiments slope steeply downwards towards the corallite margins where they become flat lying. On the axial side of the horseshoes, one or two rows of normal dissepiments are usually present.

The tabularium, which is more or less sharply delimited from the dissepimentarium, is composed of wide, flat or gently undulating plates, usually slightly downturned peripherally. The tabulae are complete or incomplete and a periaxial series of sloping plates is intermittently developed.

Insufficient material is available for a statistical study of variation in this species. The few measurements made are summarized in Table 6.

Discussion. The present material agrees very well with Edwards & Haime's (1853 : 234, pl. 52, figs. 5, 5*a*) figures and descriptions, although their original specimen appears to have had somewhat larger tabularia. Frech's (1885) figures of a specimen from the Ibergerkalk (Harz, Germany) are very close to the illustrations of the holotype and to the present material, although the horseshoe dissepiments in the German specimen appear stronger and more regularly developed.

Phillipsastrea devoniensis differs markedly from *P. hennahi* in both tabularium size and septal number. In addition, the horseshoe dissepiments of the former are somewhat less regular in size and, unlike those of *P. hennahi*, are separated from the tabularium by steep sloping normal dissepiments. The thin elongate septal dilatation in *P. devoniensis* (Pl. 4, fig. 2) also contrasts with the markedly spindle-shaped septa of *P. hennahi* (Pl. 1, fig. 1).

P. devoniensis is similar in many respects to *P. bouchardi* and *P. ibergensis*. Both the latter species, however, have slightly different tabularium structure and *P. bouchardi* has much larger tabularia (**dt** = 10–16 mm. according to Semenoff-Tian-

Chansky 1961 : 307) than *P. devoniensis*. *P. ibergensis* is further distinguished by strong spindle shaped septal dilatation.

The specimen figured by Bulvanker (1958, pl. 45, figs. 1*a*, *b*) as *P. devoniense* has considerably larger tabularia than the English material. It is closer in size to *P. bouchardi* and also has the slightly sagging tabularium structure of that species in contrast to the flat or faintly domed tabulae of *P. devoniensis*.

P. devoniensis is an uncommon species. Very few specimens have been seen in English museums and the author has found none in the field. It appears that Frech's (1885 : 67) specimen is the only record of the species from abroad.

Phillipsastrea ananas (Goldfuss)

Plate 5, figs. 1–4

1826 *Cyathophyllum ananas* Goldfuss : 60 *pars*, pl. 19, fig. 4*b*, *non* 4*a*.
1851 *Acervularia troscheli* Edwards & Haime : 416.
1885 *Phillipsastrea ananas* (Goldfuss) Frech : 49 *pars*, pl. 2, figs. 1, 2, 5, 5*a*, 5*b*, pl. 3, ?fig. 5; pl. 8, ?fig. 9.
1953 *Pseudoacervularia ananas* (Goldfuss) Różkowska : 52, text-figs. 27, 28, pl. 7, figs. 1, 2.

But not:
1881 *Heliophyllum troscheli* (Edwards & Haime); Schlüter : 203, pl. 4, figs. 3, 4.

Diagnosis. Pseudocerioid *Phillipsastrea*. Mean tabularium diameter 3·54 mm. with 14–18 major septa (East Ogwell sample). Septa thin peripherally, with slim, spindle-shaped dilatation near tabularium boundary. Major septa usually form weak axial vortex. Dissepimentarium reflexed, with imperfect series of horseshoe dissepiments at crest from which two or three rows of normal dissepiments slope steeply into tabularium. Axial tabulae flat-topped domes with peripheral horizontal concave plates.

Type specimen. The original specimen figured by Goldfuss (1826, pl. 19, fig. 4b) is either mislaid or lost. Frasnian; Namur, Belgium.

Material. BM (N.H.) R46158–9. Road cutting, south side, 30–35 yd. west of Ramsleigh Quarry entrance, East Ogwell, near Newton Abbot; Lower Frasnian.

Distribution. England: Lower Frasnian; East Ogwell, near Newton Abbot. Also widespread in Frasnian of Namur, Belgium; Harz, Stolberg near Aachen, Germany; Kielce region, Poland; Urals, Kuznetsk Basin, U.S.S.R.

Description. The material consists of fragments of apparently pseudocerioid coralla. The epitheca is predominantly straight but may be zigzagged.

The septa, both major and minor, are spindle-shaped. At the periphery they are about 0·05 mm. across but the major septa may dilate up to 0·45 mm. thick near the tabularium junction. The maximum length of septal thickening is about 2 mm. The septa may be carinate. BM (N.H.) R46159 (Pl. 5, fig. 3) has well developed yardarm carinae, up to 0·25 mm. across with a minimum spacing of 0·15 mm., on many but not all septa. BM (N.H.) R46158 (Pl. 5, fig. 2) on the other hand has only rarely developed, very faint, carinae.

The minor septa do not penetrate the tabularium but the major septa continue, much attenuated, almost to the axis where they usually form a weak vortex. There is usually an axial area 0·2–0·4 mm. in diameter which is free of septa.

The dissepiments may be uni- or multiserial between septa. The tabularium junction is not strongly marked but coincides approximately with the axial ends of the minor septa.

Table 6.—Quantitative comparison of some species and subspecies of *Phillipsastrea.*

	dt		n	n/dt	At/A
	O.R.	x̄	O.R.	x̄	x̄
P. hennahi hennahi	1·7–3·5	2·45	10–16	5·25	0·045
P. hennahi ussheri	1·2–2·5	2·04	10–14	6·16	0·063
P. devoniensis	3·0–5·0	3·72	16–23	5·04	ca. 0·1
P. ananas	3·0–4·0	3·54	14–18	4·44	ca. 0·15
P. rozkowskae	2·3–2·9	2·64	12–15	5·08	ca. 0·1

In longitudinal-section, the dissepimentarium is of variable width, and the dissepimental surface strongly reflexed with the crest on average 0·6 mm. outside the tabularium. The dissepiments at the crest are usually modified to horseshoe shape, forming a slightly discontinuous vertical series of horseshoe dissepiments. There are several rows of normal dissepiments towards the margins of the corallites and on the other side of the crest, two or three rows of dissepiments slope steeply into the tabularium.

The tabulae are complete or incomplete flat-topped domes, occupying about three-fifths of the tabularium diameter. There is a peripheral series of horizontal, distally concave plates.

The two known specimens from East Ogwell have slightly different quantitative data which is averaged in Table 6. Individually, BM (N.H.) R46159 has tabularium diameters of 3 to 3·5 mm. with 14 or 15 major septa whilst BM (N.H.) R46158 has 3·8 to 4·0 mm. tabularium diameters with 15 to 18 major septa.

Discussion. Although the two specimens described here differ slightly in some respects, they both appear to fall within the range of variation shown by *P. ananas* in areas where the species is more abundant. On the other hand, they also show some features which are intermediate in character with *P. macrommata* (F. A. Roemer).

Frech (1885 : 49) considered these two species to be synonymous whilst Różkowska (1953 : 49–52) was able to distinguish between them in Poland through the lower septal-tabularium ratio, the short, strong septal dilatation and the slightly different dissepimental arrangement in *P. macrommata.* The English material agrees in general morphological appearance with *P. ananas* of Różkowska. On the other hand, the septal insertion in both the present specimens follows more closely the curve for *P. macrommata* given by Różkowska (1957, text-fig. 26).

In view of the limited material, the two specimens are placed in *P. ananas* on morphological grounds. They may, however, need re-evaluation if a larger sample ever becomes available from East Ogwell.

Phillipsastrea rozkowskae sp. nov.

Plate 6, figs. 1–4

Derivation of name. The species is named after Professor Maria Różkowska (Poznàn, Poland).

Diagnosis. Pseudocerioid *Phillipsastrea.* Tabularium diameter 2·3–2·9 mm. with 12 to 15 major septa (topotype sample). Septa of two orders, major with short, club-shaped dilatation against tabularium boundary, becoming extremely attenuate in tabularium; minor septa hardly thickened. Dissepiments in several rows with single vertically discontinuous series of horseshoe dissepiments. Tabularium structure simple, with incomplete tabulae.

Holotype. BM(NH) R46156. Lower Frasnian; road cutting, south side, 25 yd. west of Ramsleigh Quarry entrance, East Ogwell, near Newton Abbot.

Material. BM(NH) R46156–57. Horizon and locality as for holotype.

Distribution. Type locality only.

Description. Massive, pseudocerioid colonies with predominantly pentagonal corallites separated by straight to slightly zigzagged pseudothecae. Only two fragments are available and details of colony shape, size and external features are unknown.

The septa, major and minor, are 0·05–0·15 mm. thick peripherally. They are generally straight but may occasionally be very slightly flexed in the dissepimentarium. The major septa are dilated up to 0·35 mm. across for a length of 0·6 to 1 mm. just outside the tabularium. The minor septa are only slightly thickened in the same area. The latter do not penetrate the tabularium but the major septa, extremely attenuated, extend usually to within 0·4 mm. of the axis where they are usually curved into a very faint vortex. There is no dilatation of the axial ends of the major septa. Carinae are not developed and the septa are usually smooth throughout.

Dissepiments are usually uniserial between adjacent septa. The trace of the horseshoe dissepiments, corresponding in position with the septal dilatation, forms a well marked wall around the tabularium.

In longitudinal-section, the dissepimentarium is composed of several series of variably shaped dissepiments, from near flat to quite globose. Just outside the tabularium, the dissepimental surface rises to a crest formed by a somewhat discontinuous vertical series of horseshoe dissepiments. Steep sloping vesicles are occasionally developed between the horseshoe dissepiments and the tabularium.

The structure of the tabularium is simple. Tabulae are incomplete, distally concave plates or low elongate vesicles. They are arranged to give a flat or slightly concave surface to the tabularium.

The few data available for the species are summarized in Table 6.

Discussion. *P. rozkowskae* is probably the species of *Phillipsastrea* which most closely approaches *Frechastraea.* Its septa are very similar to the typical frechastraeid form (see p. 232) and the series of horseshoe dissepiments is relatively poorly developed for *Phillipsastrea.*

P. rozkowskae is similar in its pseudocerioid growth form to *P. smithi* (Różkowska), *P. ananas* (Goldfuss) and *P. macrommata* (F. A. Roemer). It differs from the latter two, however, through its smaller tabularium size and lower **At/A** ratio as well as the character of its septal thickening. *P. smithi* is distinguished by very strong septal dilatation forming a wide, dense wall around the tabularium. On the axial side of this wall, the major septa are represented by thick lobes only, and do not cross the tabularium towards the axis.

Genus ***FRECHASTRAEA*** nov.

Derivation of name. The genus is named after Fritz Frech (1861–1917).

Diagnosis. Massive rugose corals, pseudocerioid, astraeoid or thamnasterioid. Corallites small with clearly defined wall at tabularium junction. Septa of two orders, major and minor, generally slightly thickened against tabularium junction and strongly attenuate in tabularium. In longitudinal-section, dissepiments small, globose. Septal trabeculae arranged in a fan usually on the series of dissepiments adjacent to tabularium. Horseshoe dissepiments may rarely occur in this series. Dissepimental surface almost flat with a slight elevation surrounding tabularium. Tabulae complete or incomplete.

Type species. *Cyathophyllum pentagonum* Goldfuss (1826 : 60, pl. 19, fig. 3). Frasnian; Namur, Belgium.

Distribution. Widespread in the Frasnian of Europe.

Other species assigned to *Frechastraea. Acervularia goldfussi* de Verneuil & Haime (1850 : 161); ?*Smithia boloniensis* Edwards & Haime (1851 : 423); *Smithia bowerbanki* Edwards & Haime (1851 : 423); *Smithia micrommata* C. F. Roemer (1852 : 197, pl. 5^1, figs. 20*a*, *b*); ?*Acervularia roemeri* var. *β concinna* F. A. Roemer (1855 : 32, pl. 6, figs. 19*a–c*); *Phillipsastraea sanctacrucensis* Różkowska (1953 : 59, text-figs. 32–33, pl. 2, figs. 8–10); *Phillipsastraea pentagona* (Goldfuss) var. *minima* Różkowska (1953 : 66, text-figs. 36–38, pl. 8, fig. 9).

Discussion. *Frechastraea* embraces a well defined group of Devonian colonial rugose corals. Species here included in the genus have been previously assigned to *Hexagonaria*, *Billingsastraea*, *Phillipsastrea* or synonyms of these three genera.

Workers in the last century, particularly Edwards & Haime, frequently placed pseudocerioid and astraeoid Devonian corals, including species of *Frechastraea,* in the Silurian genus *Acervularia* Schweigger. This similarity between the Silurian and Devonian forms is, however, quite superficial and *Acervularia* has long been considered unrelated to the phillipsastreids. More or less concurrent with the use of *Acervularia,* some astraeoid and thamnasterioid species of *Frechastraea* were assigned to *Smithia,* which is an objective synonym of *Phillipsastrea.*

Lang & Smith (1935 : 559) referred to *Prismatophyllum pentagona* (Goldfuss) in their remarks on the genus *Prismatophyllum. Prismatophyllum* Simpson is considered a junior synonym of *Hexagonaria* Gürich (see Lang, Smith & Thomas 1940 : 104). The type species of both, *P. prisma* Lang & Smith and *H. hexagona* (Goldfuss) respectively, are characterized by typical disphyllid dissepimentaria with the septal trabeculae sloping axially and upwards throughout. *Frechastraea* differs from these chiefly by the possession of a full trabecular fan based on the series of dissepiments adjacent to the tabularium. In addition, *Hexagonaria* shows no tendency to the development of horseshoe dissepiments and lacks the strongly defined tabularium junction characteristic of the present genus.

Many of the forms assigned to *Hexagonaria* by Moenke (1954) also do not possess a disphyllid dissepimentarium. These species, however, are morphologically quite distinct from those referred to *Frechastraea* and have been placed in *Marisastrum* by Różkowska (1965 : 262) and Scrutton (1967 : 270).

Schouppé (1958 : 235) included species of *Frechastraea* in the genus *Billingsastraea* Grabau. The type species of *Billingsastraea* is *B. verneuili* (Edwards & Haime). The holotype is missing but Ehlers & Stumm (1953 : 2) have described corals under that name which appear in all respects to satisfy the original diagnosis. *Billingsastraea sensu stricto* is thus characterized by a broadly reflexed dissepimentarium in which there is no tendency to produce horseshoe dissepiments. The septa are uniformly thin from the periphery to the axis of the corallite, usually with no sign of dilatation, and the strongly marked tabularium junction of *Frechastraea* is lacking. Oliver (1964 : 2–3) criticized Schouppé's interpretation of *Billingsastraea* and suggested that there is probably no close relationship between that genus and the phillipsastraeids. The writer subscribes to this view (Scrutton 1967 : 276) and species of *Frechastraca* are here considered quite distinct from *Billingsastraea*.

Schouppé (1958 : 156) recorded a well developed series of horseshoe dissepiments in *P. hennahi*, the type species of *Phillipsastrea*. Until that time, species of *Frechastraea* had been widely assigned to that genus. They are certainly most closely related to *Phillipsastrea* but may be distinguished from it by the rarity with which horseshoe dissepiments occur. *Frechastraea* is also strongly characterized by its septa (compare Text-figs. 4*b* & 4*c*)—uniformly thick in the dissepimentarium with a short club-shaped thickening against the tabularium boundary, and major septa strongly attenuate in the tabularium. In *Phillipsastrea* the septa are more spindle-shaped, and may be equally thin in the tabularium and peripheral parts of the dissepimentarium; frechastraeid type septa are only rarely known. Finally species of *Frechastraea* tend to have smaller individuals—seldom greater than 2mm. tabularium diameter—than species of *Phillipsastrea*.

The occasional horseshoe dissepiments developed in the dissepimentaria of species of *Frechastraea* are recorded here for the first time. It is thought that the genus descended from a phillipsastreid ancestor chiefly through the progressive elimination of horseshoes from the dissepimentarium. *P. rozkowskae*, in particular, shows a tendency toward frechastraeid characters and is considered a possible intermediary between the two genera. It may be significant in an evolutionary sense that Różkowska (1953) did not record horseshoes in species of *Frechastraea* from mainly Upper Frasnian horizons in Poland whilst they can often be seen in the dissepimentaria of the same species among the English Lower Frasnian material.

Frechastraea pentagona pentagona (Goldfuss)

Plate 6, fig. 5; Plate 7, figs. 1–5

1826 *Cyathophyllum pentagonum* Goldfuss : 60, pl. 19, fig. 3.
1840 *Astrea* (*Favastrea*) *pentagona* (Goldfuss) Lonsdale : 697 *pars*, pl. 58, fig. 1 (*non* 1*a*).
1841 *Astrea pentagona* (Goldfuss); Phillips : 11, pl. 6, fig. 15.
1851 *Acervularia pentagona* (Goldfuss) Edwards & Haime : 418.
1853 *Acervularia pentagona* (Goldfuss); Edwards & Haime : 238, pl. 53, figs. 5–5*b*.
1883 *Acervularia pentagona* (Goldfuss); C. F. Roemer : 352, text-fig. 70.
1885 *Phillipsastrea pentagona* (Goldfuss) Frech : 54 *pars*, pl. 3, figs. 7, 7*a*, ?8, 10; pl. 8, fig. 3.
1935 *Prismatophyllum pentagona* (Goldfuss) Lang & Smith : 559.
1953 *Phillipsastraea pentagona* (Goldfuss); Różkowska : 64, text-figs. 36–39, pl. 8, fig. 7.

But not:
1952 *Phillipsastraea pentagona* (Goldfuss); Soshkina : 102, pl. 43, fig. 145.

DIAGNOSIS. Pseudocerioid *Frechastraea* with mean tabularium diameter 1·09 mm. and 7 to 13 major septa (East Ogwell sample). Smooth, non-carinate septa. Horseshoe dissepiments very rarely developed. Tabulae complete or incomplete. Increase axial or lateral.

LECTOTYPE (selected by J. W. Pickett *in press*). Original of Goldfuss 1826, pl. 19, fig. 3 which is specimen 206 in the Goldfuss Collection of the Geologisch-Paläontologisches Institut, Bonn. Goldfuss (1826 : 60) gave the horizon and locality as the " Transition limestone of the Namur region ", Belgium. Frasnian.

MATERIAL. Ramsleigh Quarry: OUM D279 (Colony 1), BM(NH) R23400 (Colony 3), BM(NH) R5635 (Colony 4). Other measured specimens: BM(NH) R676, TM(JB) 305A.

Road cutting, 20 yd. west of Ramsleigh Quarry entrance: OUM D538 (Colony 2). Other measured specimen: OUM D537.

Road cutting, 40 yd. west of Ramsleigh Quarry entrance. Measured specimen: OUM D532.

DISTRIBUTION. England: Lower Frasnian limestones, Ramsleigh Quarry and adjacent road cutting, East Ogwell, near Newton Abbot, south Devon. Also Frasnian of Belgium, Germany and Poland.

DESCRIPTION. Colony shape, external features and overall dimensions are unknown as all the English material is fragmentary. Różkowska (1953 : 64), however, described Polish representatives of this subspecies as thick, tabular colonies up to 6 cm. in diameter and 6 cm. in height. Goldfuss' original specimen is a thick, rectangular block with the convex upper surface measuring 7 cm. by 8 cm. The corallites have slightly depressed tabularia with a low, encircling ridge formed by the innermost series of dissepiments. Różkowska gave no details of a holotheca and it is not preserved in any of the English specimens.

The colonies are massive, pseudocerioid, tending rarely to astraeoid or thamnasterioid. Individual corallites, usually pentagonal or hexagonal in shape, are separated from each other by a straight or zigzagged pseudotheca. Occasionally the pseudotheca may break down when the septa are more or less confluent from one corallite to the next.

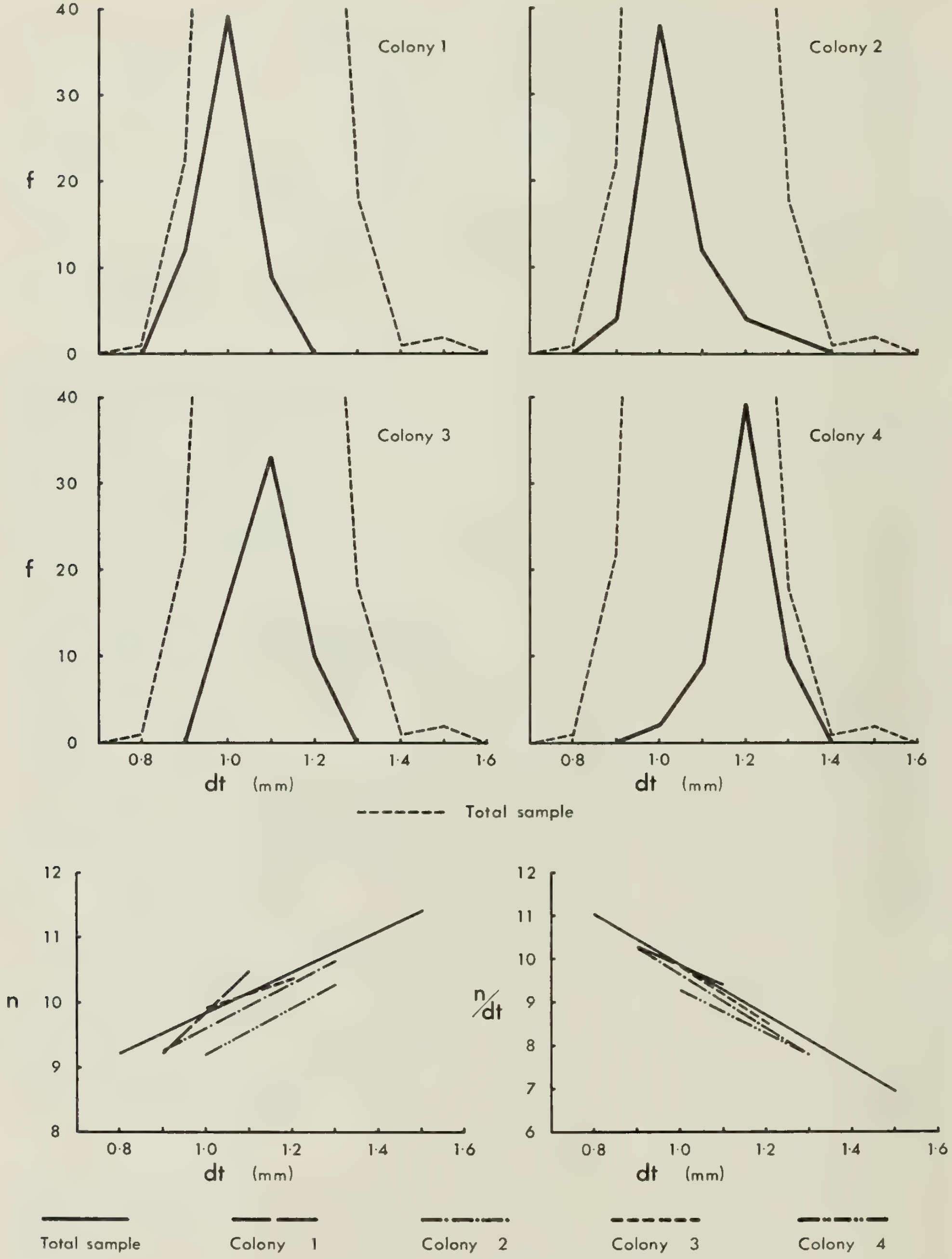


FIG. 13. *Frechastraea pentagona pentagona.*

TABLE 7.—Statistical data for some characters of *Frechastraea pentagona pentagona.*

		Total sample	Colony 1	Colony 2	Colony 3	Colony 4
	N	424 (8)	60	60	60	60
dt	**O.R.**	0·8–1·5	0·9–1·1	0·9–1·3	1·0–1·2	1·0–1·3
	$\bar{x}$	1·09	1·00	1·04	1·09	1·20
	s	0·10	0·059	0·084	0·067	0·068
	C.V.	9·38	5·97	8·13	6·12	5·65
	S.E.$_m$	0·005	0·0077	0·011	0·0086	0·0087
n	**O.R.**	7–12	7–11	8–11	9–12	9–12
	$\bar{x}$	10·12	9·80	9·73	10·12	9·90
	s	0·32	0·38	0·30	0·15	0·24
	C.V.	3·15	3·85	3·04	1·48	2·43
	S.E.$_m$	0·016	0·049	0·038	0·019	0·031
n/dt	**O.R.**	6·67–12·00	7·78–11·11	7·69–10·00	8·33–10·00	7·50–10·00
	$\bar{x}$	9·36	9·86	9·73	9·32	8·30
	s	0·59	0·25	0·30	0·44	0·33
	C.V.	6·34	2·54	3·04	4·69	3·93
	S.E.$_m$	0·029	0·032	0·038	0·056	0·042
Graphs:—						
n/dt	**r**	0·92	0·94	0·74	0·99	0·91
	a	3·13	6·35	3·51	2·25	3·57
	b	6·72	3·49	6·09	7·67	5·63
n/dt/td	**r**	−1·00	−0·90	−0·96	−0·99	−0·94
	a	−5·81	−4·21	−6·10	−6·56	−4·83
	b	15·68	14·05	15·75	16·42	14·07

	A	**At**	**At/A**	Graph:—**At/A**	
O.R.	0·091–0·16	0·0078–0·011	0·057–0·099		
$\bar{x}$	0·12	0·0093	0·079	**r**	0·38
s	0·024	0·0013	0·015	**a**	0·055
C.V.	20·25	14·38	18·63	**b**	0·0027
S.E.$_m$	0·0086	0·00047	0·0052		

The septa, both major and minor, are straight and uniformly thick, about 0·05 mm. across, in the dissepimentarium. At the tabularium junction the major septa, and to a lesser degree the minor, are dilated to form a short bulbous thickening. This thickening, associated with the clearly defined junction between tabulae and dissepiments, gives rise to a strong internal wall at this point. The minor septa are normally confined to the dissepimentarium and only occasionally show as slight projections into the tabularium. The major septa, however, continue into the tabularium as extremely thin processes, usually extending halfway or slightly more towards the axis and sometimes reaching the axis itself. There is a strong tendency for the axial ends of the longer major septa to fuse. The thin septal elements in the tabularium are easily obliterated by slight recrystallization, but even in the best of the material examined there was no sign of thickening of the axial ends of the major septa.

The dissepiments are almost always uniserial between adjacent septa and appear moderately spaced in cross-section. In longitudinal-section, the dissepimentarium is composed of several series of small, evenly developed, well arched dissepiments. Their vertical height varies between 0·1 and 0·2 mm. The dissepimental surface is usually flat but may occasionally slope slightly away from the tabularium boundary. At the latter position, a dissepiment may very rarely be modified into a horseshoe shape but there is no tendency to develop a series of horseshoe dissepiments. No more than two, or possibly three horseshoes have been observed in continuous vertical succession.

The tabularium structure is often partially obscured by slight recrystallization. The tabulae are usually flat lying and may be complete or interleaved. Occasionally, however, they slope downwards away from from the axis with an overall tent or bell shaped appearance. In some cases there is evidence of axial structures suggesting the vesicles described in the tabularium of *Frechastraea goldfussi* (see p. 249). Unfortunately, poor preservation and sometimes septal traces obscure the axial area at these points and the relationships of the tabulae are not clear. In the more simply constructed tabularia, the tabulae have an average vertical spacing of about 0·2 mm.

Both axial and lateral increase have been observed in this subspecies, the latter being more common.

A sample of eight colonies from the limestones exposed in Ramsleigh Quarry and the adjacent road cutting has been statistically analysed. Four of the colonies have also been analysed individually. The statistics are listed in Table 7 and illustrated graphically in Text-figs. 13 and 16.

DISCUSSION. Both Lonsdale (1840 : 697) and Frech (1885 : 54) included *Acervularia goldfussi* or specimens belonging to this species in their interpretation of *Cyathophyllum pentagonum*. The two species are superficially extremely similar, although on close inspection they can be readily distinguished. The details of the differences are given below (p. 253) under *F. goldfussi*.

The most recent thorough investigation of *Frechastraea pentagona pentagona* is by Różkowska (1953 : 64) as a species of *Phillipsastrea*. Her material has a slightly larger mean tabularium diameter than the English sample but there is no doubt that they belong to the same subspecies.

Frechastraea pentagona (Goldfuss) ***minima*** (Różkowska)

Plate 8, figs. 1–3

1953 *Phillipsastraea pentagona* (Goldfuss) var. *minima* Różkowska : 66, text-figs. 36–38, pl. 8, fig. 9.

1953 *Phillipsastraea bowerbanki* (Edwards & Haime); Różkowska : 67, pl. 8, figs. 3, 4.

1959 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Middleton : 156, text-fig. 6*f*.

DIAGNOSIS. Pseudocerioid to astraeoid to thamnasterioid *Frechastraea*. Mean tabularium diameter 0·96 mm. with 7 to 12 major septa (East Ogwell sample).

Tabularia somewhat unevenly spaced. Septa sinuous and only slightly dilated at tabularium junction. Horseshoe dissepiments rare. Increase axial or lateral.

HOLOTYPE. A98 in the Collections of the Polska Akademia Nauk, Pracownia Palaeozoologii, Poznàn, Poland. Upper Frasnian, Psie Górki, Kielce, Poland.

MATERIAL. Ramsleigh Quarry: GSM 73119 (Colony 1), GSM 11822 (Colony 2), GSM 73118 (Colony 3). Other measured specimens: BM(NH) R46371, BM(NH) R23266. Additional material: GSM 11821, GSM 11823.

DISTRIBUTION. England: Lower Frasnian of Ramsleigh Quarry, East Ogwell, near Newton Abbot, south Devon. Also Upper Frasnian of Kielce, Poland.

DESCRIPTION. Details of size, shape and external features of the English material are unknown as it is fragmentary. Różkowska (1953 : 67), however, described the holotype as a low, plate-like colony measuring 3·5 cm. by 1·6 cm. in surface area.

Individual corallites are seldom completely surrounded by an external pseudotheca and usually the septa are confluent or subconfluent between them. All gradations from the pseudocerioid to the thamnasterioid stage are usually present in the same colony and this is accompanied by a general increase in the distances separating the tabularia. Where an external pseudotheca is present, it is formed by the deflection of the peripheral septal ends.

The septa, 0·05 mm. or less in thickness, are uniformly thin and are gently sinuous between tabularia. They are usually smooth sided. Rarely there appears to be a slight separation of the trabeculae, which remain unthickened, resulting in discontinuous septa. At the tabularium junction, the septa are slightly dilated for about 0·1 mm. of their length. Within the tabularium, the major septa thin abruptly and continue as very fine filaments more or less to the axis, where the ends of two or more adjacent septa may fuse. The minor septa do not penetrate into the tabularium.

The dissepiments are almost always uniserial between adjacent septa. The tabularium junction is sharply defined in cross-section, giving the appearance of an internal wall.

In longitudinal-section, the dissepimentarium is composed of several series of small, well arched dissepiments. They may vary somewhat in size and their height, usually about 0·1 mm., ranges from 0·05 to 0·25 mm. The surface of the dissepimentarium is flat peripherally, usually rising slightly with the more globose dissepiments adjacent to the tabularium. Horseshoe dissepiments may rarely develop in the latter position.

The tabularium structure is simple and the tabulae may be complete or incomplete. The complete tabulae are either flat or sag slightly in the middle. The incomplete tabulae are flat to slightly bowed and interleaved with each other, or in the form of long weakly arched vesicles. The vertical spacing of the tabulae may vary between 0·1 and 0·3 mm., but is normally about 0·15 mm. in the more regularly developed tabularia.

Examples of both axial and lateral increase have been observed.

A statistical analysis has been made of a total sample of 5 colonies from Ramsleigh

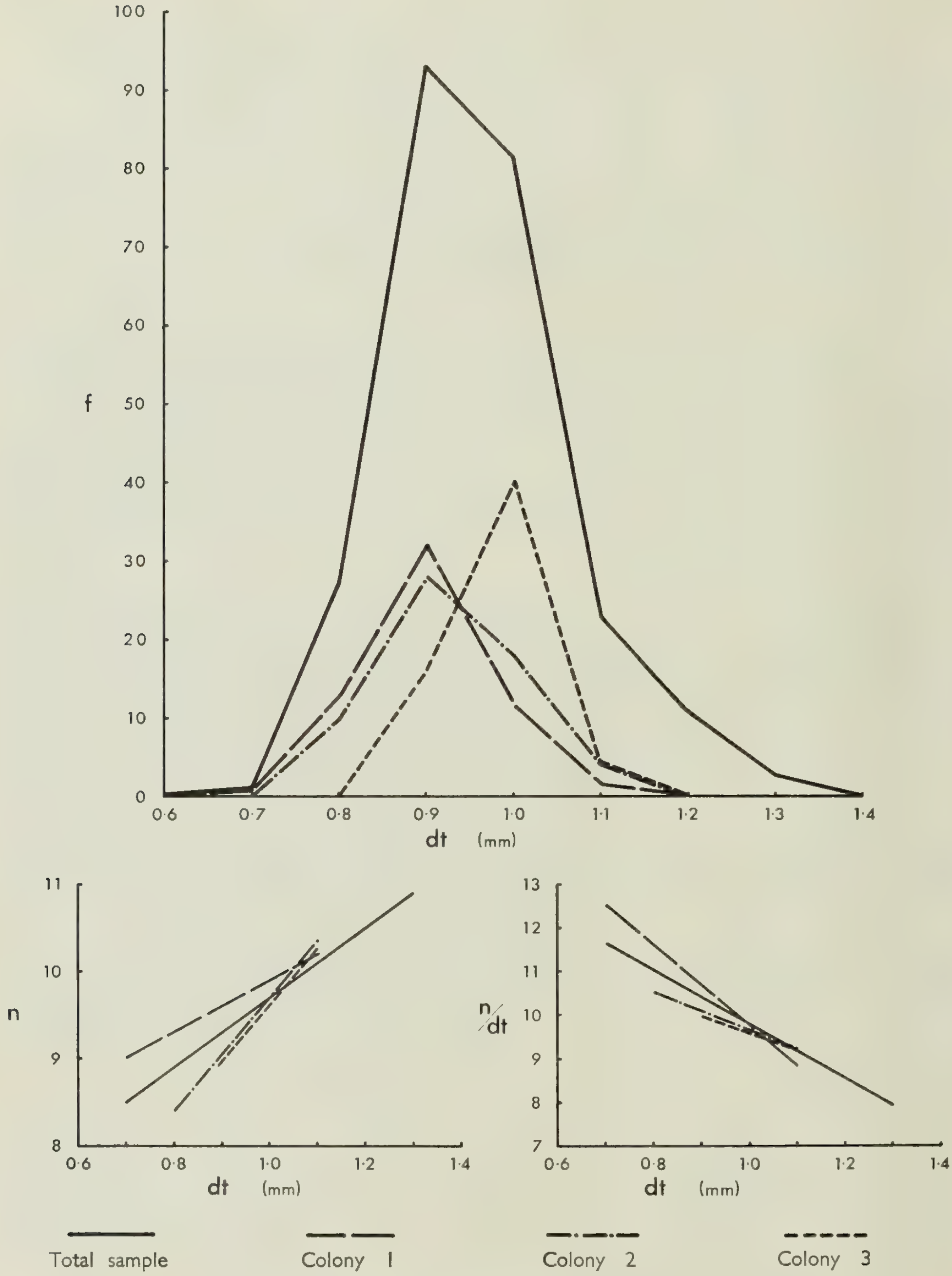


FIG. 14. *Frechastraea pentagona minima.*

Table 8.—Statistical data for some characters of *Frechastraea pentagona minima.*

		Total sample	Colony 1	Colony 2	Colony 3
	N	240 (5)	60	60	60
	O.R.	0·7–1·3	0·7–1·1	0·8–1·1	0·9–1·1
	$\bar{x}$	0·96	0·90	0·93	0·98
dt	**s**	0·11	0·079	0·082	0·055
	C.V.	10·98	8·78	8·85	5·57
	S.E.$_m$	0·0068	0·010	0·011	0·0071
	O.R.	7–12	8–10	7–11	8–10
	$\bar{x}$	9·54	9·61	9·25	9·52
n	**s**	0·42	0·23	0·54	0·36
	C.V.	4·42	2·42	5·86	3·77
	S.E.$_m$	0·027	0·030	0·070	0·046
	O.R.	7·69–12·87	8·18–12·87	7·78–11·26	8·89–11·12
	$\bar{x}$	10·05	10·72	10·01	9·72
n/dt	**s**	0·64	0·73	0·35	0·20
	C.V.	6·40	6·82	3·54	2·04
	S.E.$_m$	0·42	0·094	0·046	0·026
Graphs:—					
	r	0·98	0·77	0·95	0·97
n/dt	**a**	4·00	2·94	6·61	6·58
	b	5·71	6·96	3·12	3·07
	r	−0·98	−0·99	−0·88	−0·92
n/dt / dt	**a**	−6·11	−9·24	−4·32	−3·63
	b	15·91	19·06	14·01	13·27

	A	**At**	**At/A**	Graph:—**At/A**	
O.R.	0·11–0·15	0·0065–0·010	0·054–0·071		
$\bar{x}$	0·12	0·0075	0·062	**r**	0·84
s	0·017	0·0016	0·0076	**a**	0·092
C.V.	14·52	21·37	12·21	**b**	−0·0036
S.E.$_m$	0·0078	0·00072	0·0034		

Quarry. Three of these colonies have also been analysed individually. The statistics are listed in Table 8 and illustrated graphically in Text-figs. 14 and 16.

Discussion. Różkowska (1953 : 66) erected this subspecies as a variety of "*Phillipsastraea pentagona*" on only one specimen. Although the tabularia of her specimen (0·6–0·8 mm. diameter) are slightly smaller than those in the English examples, the colonies are in complete morphological agreement and are undoubtedly the same subspecies. The holotype clearly shows the characteristic pseudocerioid grading to thamnasterioid nature of the corallites and the irregular spacing of the tabularia described above.

The specimen described by Różkowska (1953 : 67) as "*Phillipsastraea bowerbanki*" is indistinguishable from GSM 73118 (Pl. 8, fig. 1) of the present material and is thus also referable to this subspecies. The slight morphological differences between these specimens and the holotype of *F. pentagona minima* lie within the range of variation to be expected. *F. pentagona minima* is quite distinct from *F. bowerbanki* which is almost exclusively thamnasterioid and has considerably larger tabularia, wide and regularly spaced (see p. 253).

Two fragments from Ramsleigh Quarry (GVM 26/7 and 26/8), misidentified as *Phillipsastraea pentagona* var. *micrommata* by Middleton (1959 : 156), also belong to this subspecies.

F. pentagona pentagona and *F. pentagona minima* are very similar in quantitative terms. Only 0·13 mm. separates their mean tabularium diameters. In addition, their lines on the graphs plotting septal number against tabularium diameter and tabularium area against corallite area are very similar in both slope and position (Text-fig. 16). Nevertheless, because of the large sample sizes, tests of statistical discrimination show the subspecies to differ significantly in both **dt** (Table 10) and their lines on the former of the two graphs.

F. pentagona minima is distinguished principally on qualitative characteristics, and without prior separation on these grounds, could not be differentiated from *F. pentagona pentagona* on quantitative data alone. *F. pentagona pentagona* is pseudocerioid, tending slightly to astraeoid, with straight septa. The septa in *F. pentagona minima*, on the other hand, are generally sinuous and associated with a wide range in form from pseudocerioid to thamnasterioid. The tabularia also tend to be irregularly spaced. In the material so far examined, no difficulty has been found in distinguishing quite clearly between the two subspecies.

Both occur in association in the Lower Frasnian Ramsleigh limestones in England and the Upper Frasnian of Kielce in Poland (Różkowska 1953). In the English fauna, *F. pentagona pentagona* and *F. pentagona minima* occur in approximately equal numbers whilst Różkowska's figures suggest a ratio of 11 : 1 in favour of *F. pentagona pentagona* in the Kielce area.

Frechastraea micrommata (C. F. Roemer)

Plate 8, figs. 4, 5

1852 *Smithia micromata* C. F. Roemer : 197, pl. 5^1, figs. 20*a*, *b*.

But not:

1885 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer) Frech : 56, pl. 3, figs 11–13; pl. 8, fig. 1.

1953 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Różkowska : 66, text-figs. 36–38; pl. 8, fig. 8.

1958 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Bulvanker : 123, pl. 60, figs. 1–3; pl. 61, figs. 4, 5.

1959 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Middleton : 156, text-fig. 6*f*.

DIAGNOSIS. Pseudocerioid tending to astraeoid *Frechastraea*. Mean tabularium diameter 1·42 mm. with 18 to 21 septa (holotype). Major and minor septa not distinguished as septa penetrating the tabularium exceedingly rare; septa non-carinate. Tabularium structure very simple, usually composed of complete tabulae. Increase lateral.

Lectotype (here chosen). Specimen no. 34 in the collections of the Geologisch-Paläontologisches Institut, Bonn. Original of Roemer's (1852, pl. 5^1) figures 20*a*, *b*. Frasnian; Ferques near Boulogne, France.

Description. Colony irregularly disc shaped, 8 cm. in diameter and 4 cm. high; covered basally by a strongly concentrically ridged holotheca. The corallites are pseudocerioid tending to astraeoid with a thin, usually zigzagged, pseudotheca.

The septa are not normally distinguished as major and minor as with very rare exceptions they all end at the tabularium junction. The septa are about 0·05 mm. thick in the dissepimentarium and follow a straight or slightly sinuous course to the tabularium boundary where they may thicken slightly. Septa may occasionally form slight inward projections on the tabularium boundary and one septum was seen to penetrate the tabularium for a distance of 0·4 mm.

The tabularium-dissepimentarium junction is a thin strong circular wall in cross-section. This wall appears to be the product of septal dilatation and thickening of the inner arms of the series of dissepiments adjacent to the tabularium. Sometimes, however, the septa themselves appear to bend sharply at the boundary to form a segment of the wall.

In longitudinal-section, the dissepimentarium is composed of several series of quite globose dissepiments normally 0·5–0·6 mm. in height. In narrow levels which can be traced from corallite to corallite, however, they become smaller, flatter and more closely spaced. The dissepimental surface is flat over most of its area but rises slightly to a crest adjacent to the tabularium. Horseshoe dissepiments have not been observed.

Tabularium structure is very simple, consisting in the main of complete flat or slightly bowed tabulae with occasional incomplete arched plates. The latter may be subsidiary to the complete tabulae or may interleaf to form the tabularium structure proper.

One example of lateral increase has been observed.

Measurements on twelve corallites showed tabularium diameter to range from 1·3–1·5 mm., mean value 1·42 mm., with 18 to 21 septa. Mean **n/dt**, taking **n** to be half the number of septa in each corallite, is 6·94.

Discussion. The above description is based on Roemer's figured specimen only. Although no horseshoe dissepiments have been observed, the character of the species as a whole places it without doubt in *Frechastraea*. Full knowledge of the variation in dissepimental shape must await the description of further material belonging to this species.

This is the first time that the type specimen has been sectioned and the slides show that Frech (1885 : 56) and subsequent authors have misidentified the species. The specimens placed by Frech and others in *Smithia micrommata* (as *Phillipsastrea pentagona* var. *micrommata*) are here assigned to *F. carinata* sp. nov. which is described below.

F. micrommata differs from all other known species of *Frechastraea* by the lack of any distinction between major and minor septa. In particular, it can be distinguished from *F. carinata* by the latter's septal carination and more complex tabularium structure. Data so far available show that tabularia in *F. micrommata* are somewhat larger than in *F. carinata* ($\mathbf{dt\bar{x}} = 1{\cdot}02$ mm.).

Frechastrea carinata sp. nov.

Plate 9, figs. 1–3

1885 *Phillipsastrea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer) Frech : 56, pl. 3, figs. 11–12, ?13; pl. 8, ?fig. 1.
1953 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Różkowska : 66, text-figs. 36–38, pl. 8, fig. 8.
But not:
1852 *Smithia micrommata* C. F. Roemer : 197, pl. 5^1, figs. 20*a*, *b*.
1958 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Bulvanker : 123, pl. 60, figs. 1–3; pl. 61, figs. 4–5.
1959 *Phillipsastraea pentagona* (Goldfuss) var. *micrommata* (C. F. Roemer); Middleton : 156, text-fig. 6*f*.

Derivation of name. The name refers to the presence of septal carinae, an important distinguishing feature of this species.

Diagnosis. Pseudocerioid, tending to astraeoid and thamnasterioid *Frechastraea*. Mean tabularium diameter 1·02 mm. and between 8 and 14 major septa (topotype sample). Septa variably but typically carinate. Horseshoe dissepiments very rare. Tabulae mainly incomplete. Increase axial or lateral.

Holotype. OUM D309. Lower Frasnian; road cutting, 80 yd. west of Ramsleigh Quarry entrance, East Ogwell, near Newton Abbot, south Devon.

Material. Ramsleigh Quarry: BM(NH) R23210 (Colony 1), BM(NH) R23211 (Colony 2), BM(NH) R23216 (Colony 3), BM(NH) R5640 (Colony 4). Other measured specimens: BM(NH) R677, BM(NH) R5634.

Road cutting, 80 yd. west of Ramsleigh Quarry entrance. Measured material: OUM D309–310, OUM D535–6.

Distribution. England: Lower Frasnian limestones, Ramsleigh Quarry and the adjacent road cutting, East Ogwell, near Newton Abbot, south Devon. Also Frasnian of Germany (Harz) and Poland (Kielce).

Description. Nothing is known of colony shape, size and external features from the present material.

The colonies are pseudocerioid, tending to astraeoid and occasionally thamnasterioid in parts. Corallites are irregularly polygonal, usually pentagonal or hexagonal, and for the most part separated from each other by a straight or slightly zigzagged wall formed by the deflection of the peripheral septal ends. When this pseudotheca breaks down, the geniculate ends of the septa are more or less confluent with those of the adjacent corallite.

The septa, of two orders major and minor, are variable in thickness but average about 0·05 mm. in the dissepimentarium where they may be sinuous. Occasionally corallites have a bilateral appearance when the septa tend to lie parallel on either side of the tabularium. Within the tabularium, the major septa thin considerably to about 0·02 mm. in thickness and continue, as straight or flexuous filaments, more or less to the axis. Minor septa are confined to the dissepimentarium. Sometimes the axial ends of adjacent major septa fuse, or the axial ends of opposite septa are continuous across the tabularium. Signs of thickening of the axial ends of septa are very rare.

The septa are variably carinate in the dissepimentarium. In exceptional cases the carinae may reach 0·4 mm. in width, but mostly they are between 0·1 and 0·15 mm. Their spacing varies but normally there are 10 carinae per mm. of septal length. On individual septa, carination is heaviest in a zone of irregular width surrounding the tabularium, corresponding to the septal dilatation observed in *Frechastraea pentagona* and *F. goldfussi*; occasionally, adjacent carinae may fuse along the septa in this zone. As they enter the tabularium, the septa rapidly become smooth.

The dissepiments, moderately to closely spaced in cross-section, are almost exclusively uniserial between adjacent septa. The tabularium junction is sharply defined.

In longitudinal-section the dissepimentarium consists of several series of regularly developed, small, arched dissepiments. Their height is usually between 0·1 and 0·2 mm. The dissepiments become progressively more globose towards the tabularium and against the tabularium boundary, horseshoe dissepiments occur very rarely. The surface of the dissepimentarium slopes slightly downwards and outwards from the tabularium and is flat lying peripherally.

The tabularium structure is usually simple. The tabulae are commonly incomplete and may be flat or moderately arched. Their vertical spacing averages about 0·2 mm. In one specimen, OUM D310b, there is evidence of highly domed axial plates, occupying about one fifth of the tabularium diameter, with peripheral flat, or slightly bowed tabulae. This axial structure is not clearly developed but it appears to be similar to that described in *F. goldfussi*.

Very few instances of increase have been observed but both axial and lateral are represented.

A total sample of ten colonies from Ramsleigh Quarry and the adjacent road cutting has been statistically analysed. Four of the colonies have also received individual treatment. The statistics are listed in Table 9 and illustrated graphically in Text-figs. 15, 16.

DISCUSSION. Material assigned to this new species was formerly known, due to Frech's (1885 : 56) work, as '*Phillipsastrea pentagona* var. *micrommata* (C. F. Roemer)'. Recently, however, the writer has been able to section Roemer's figured specimen of *Smithia micrommata*, which is described above. This shows conclusively that Frech and all subsequent workers have wrongly interpreted Roemer's species.

Frech also placed *Acervularia roemeri* var. *β concinna* F. A. Roemer in synonymy with his *P. pentagona* var. *micrommata*. The original material of the former variety appears to be missing and F. A. Roemer's illustrations (1855, pl. 6, figs. 19*a–c*) are

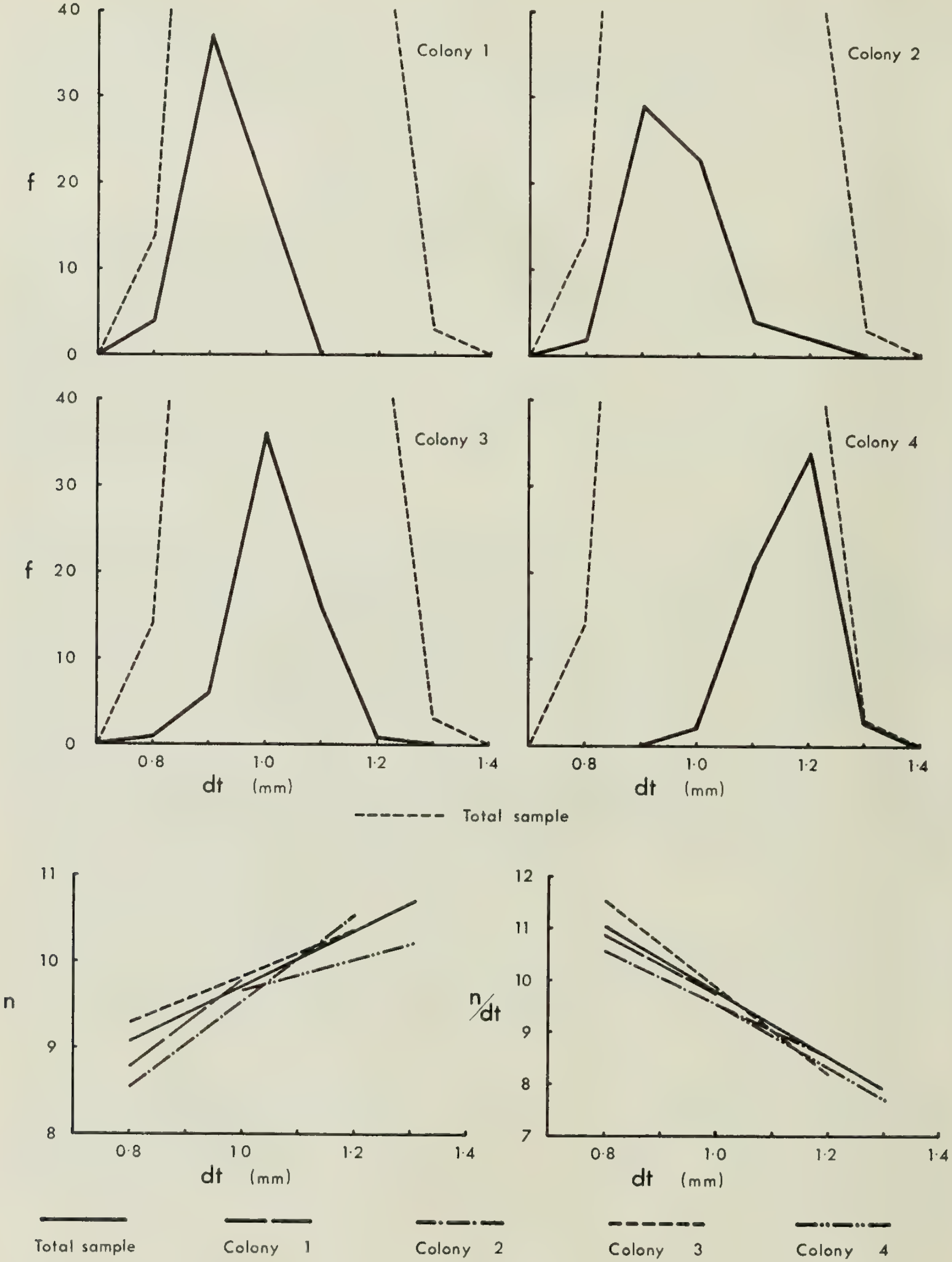


FIG. 15. *Frechastraea carinata.*

rather poor. They show no sign of septal carinae, however, and the septa themselves are spindle-shaped and thin peripherally—the phillipsastreid rather than the frechastraeid pattern. The present material is thus considered distinct from *A. roemeri* var. *β concinna*.

F. carinata is extremely close quantitatively to *F. pentagona*, with its mean tabularium diameter falling between that of *F. pentagona pentagona* and *F. pentagona minima* (Text-fig. 16). Statistical discrimination however reflects the high sample

TABLE 9.—Statistical data for some characters of *Frechastraea carinata*.

		Total sample	Colony 1	Colony 2	Colony 3	Colony 4
	N	423 (9)	60	60	60	60
dt	**O.R.**	0·8–1·3	0·8–1·0	0·8–1·2	0·8–1·2	1·0–1·3
	$\bar{x}$	1·02	0·93	0·96	1·02	1·16
	s	0·11	0·057	0·081	0·069	0·064
	C.V.	10·56	6·18	8·44	6·81	5·47
	S.E.$_m$	0·0052	0·0074	0·010	0·0090	0·0082
n	**O.R**	8–14	8–10	8–11	8–11	9–11
	$\bar{x}$	9·75	9·42	9·35	9·87	9·95
	s	0·34	0·29	0·40	0·19	0·12
	C.V.	3·51	3·07	4·29	1·89	1·18
	S.E.$_m$	0·017	0·037	0·052	0·024	0·015
n/dt	**O.R.**	7·27–12·73	8·89–11·26	8·00–11·11	8·33–12·50	7·50–12·50
	$\bar{x}$	9·66	10·20	9·79	9·74	8·57
	s	0·68	0·32	0·41	0·58	0·39
	C.V.	7·07	3·13	4·22	5·90	4·50
	S.E.$_m$	0·033	0·041	0·053	0·074	0·050
Graphs:—						
n/dt	**r**	0·95	1·00	0·93	0·70	0·89
	a	3·18	5·07	4·96	2·69	1·84
	b	6·52	4·73	4·60	7·13	7·82
n/dt / dt	**r**	−1·00	−1·00	−0·96	−0·96	−1·00
	a	−6·36	−5·59	−5·11	−8·30	−6·06
	b	16·12	15·37	14·69	18·18	15·62

	A	**At**	**At/A**	Graph:—**At/A**	
O.R.	0·10–0·17	0·0067–0·011	0·052–0·088		
$\bar{x}$	0·13	0·0082	0·063	**r**	0·77
s	0·024	0·0013	0·011	**a**	0·054
C.V.	18·45	15·86	17·68	**b**	0·0012
S.E.$_m$	0·0081	0·00044	0·0037		

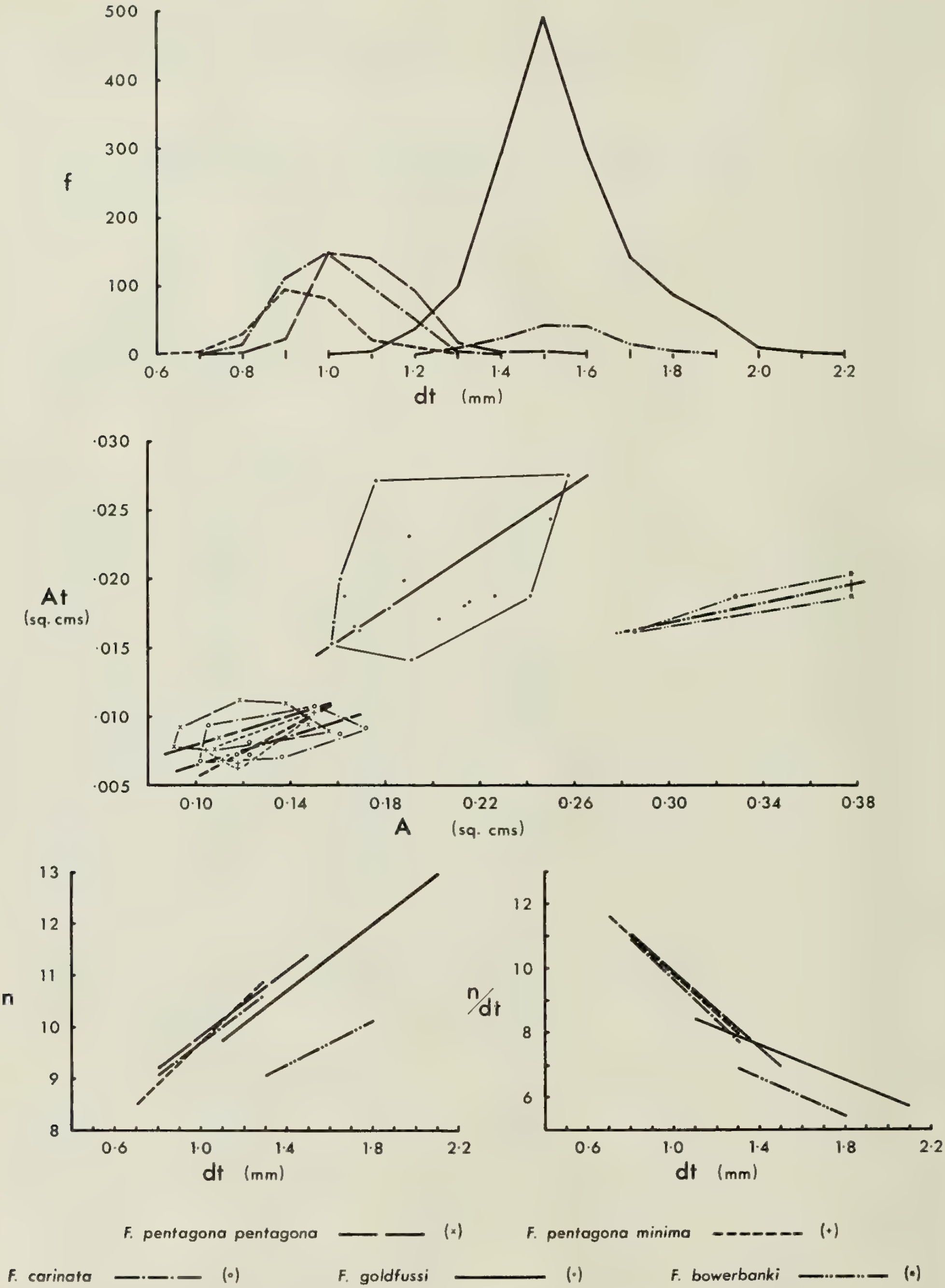


FIG. 16. Graphical comparison of some quantitative characters for the species and subspecies of *Frechastraea*.

Table 10.—Statistical discrimination between some characters for species and subspecies of *Frechastraea*. Significant values in bold; s = slope, p = position.

			pentagona pentagona	*pentagona minima*	*carinata*	*goldfussi*	*bowerbanki*
Values of "**t**":—							
dt	*pentagona pentagona*			**15·388**	**9·838**	**55·924**	
	pentagona minima		**15·388**		**6·589**		
	carinata		**9·838**	**6·589**			
	goldfussi		**55·924**				0·149
	bowerbanki					0·149	
Values of "**z**":—							
n/dt	*pentagona pentagona*	s		**11·041**	0·724		
		p			**6·946**		
	pentagona minima	s	**11·041**		**11·335**		
		p					
	carinata	s	0·724	**11·335**		1·562	
		p	**6·946**			**10·426**	
	goldfussi	s			1·562		**13·855**
		p			**10·426**		
	bowerbanki	s				**13·855**	
		p					
At/A	*pentagona pentagona*	s		1·326	0·379	2·196	
		p		0·116	**4·533**	**3·724**	
	pentagona minima	s	1·326		1·544	0·719	
		p	0·116		0·000	**3·496**	
	carinata	s	0·379	1·544			
		p	**4·533**	0·000			
	goldfussi	s	2·196	0·719			**3·719**
		p	**3·724**	**3·496**			
	bowerbanki	s					
		p				**3·719**	

sizes and *F. carinata* can be shown to be significantly different from both subspecies in **dt** and the plot of **n** against **dt**, and from *F. pentagona pentagona* alone in the plot of **At** against **A** (Table 10).

Qualitatively, *F. carinata* is distinguished by its sinuous, variably carinate septa. There is also a characteristic tendency for the majority of the septa in one corallite to follow the same directional trend in the dissepimentarium. *F. sanctacrucensis* (Różkowska), recorded so far only from Poland, is closest in general appearance to *F. carinata*. The former is clearly astraeoid, however, with considerably larger tabularia (**dt** *ca.* 2 mm., **n** 12–14), and its septal carination gives a distinctive " string-of-pearls " effect.

Frechastraea goldfussi (de Verneuil & Haime)

Plate 10, figs. 1–5; Plate 11, figs. 1, 2

1826 *Cyathophyllum ananas* Goldfuss : 60 *pars*, pl. 19, fig. 4*a* (*non* fig. 4*b*).
1840 *Astrea* (*Favastrea*) *pentagona* (Goldfuss) Lonsdale : 697 *pars*, pl. 58, fig. 1*a* (*non* fig. 1).
1850 *Acervularia goldfussi* de Verneuil & Haime : 161.

1851 *Acervularia goldfussi* de Verneuil & Haime; Edwards & Haime : 417.
1851 *Acervularia limitata* Edwards & Haime : 419.
1853 *Acervularia goldfussi* de Verneuil & Haime; Edwards & Haime : 236, pl. 53, figs. 3, 3*a*.
1853 *Acervularia limitata* Edwards & Haime; Edwards & Haime : 238, pl. 54, ?figs. 1, 1*a*.
1881 *Acervularia pentagona* (Goldfuss); Schlüter : 89, pl. 9, figs. 4, 5.
1883 *Acervularia goldfussi* de Verneuil & Haime; C. F. Roemer : 352.
1883 *Acervularia limitata* Edwards & Haime; C. F. Roemer : 353.
1885 *Phillipsastrea ananas* (Goldfuss) Frech : 49 *pars*.
1885 *Phillipsastrea pentagona* (Goldfuss) Frech : 54, *pars*, pl. 3, ?figs. 6, 9.
1951 *Phillipsastraea limitata* (Edwards & Haime); Soshkina : 97, pl. 17, fig. 2; pl. 18, fig. 2; pl. 23, fig. 4.
1952 *Phillipsastraea limitata* (Edwards & Haime); Soshkina : 101, pl. 42, fig. 142.
1953 *Phillipsastraea goldfussi* (Edwards & Haime); Różkowska : 62, text-figs. 35–37, pl. 8, figs. 5, 6.
1958 *Billingsastraea goldfussi* (Edwards & Haime) Schouppé : 236, text-figs. 25, 26.
1959 *Phillipsastraea goldfussi* (Edwards & Haime); Middleton : 156, text-fig. 6*d*.

But not:
1881 *Heliophyllum* cf. *limitatum* (Edwards & Haime) Schlüter : 87, pl. 8, figs. 1, 2.

DIAGNOSIS. Pseudocerioid *Frechastraea*. Mean tabularium diameter 1·53 mm. and between 7 and 17 major septa (East Ogwell sample). Septa smooth, very rarely carinate, usually with lobate thickening on axial ends of major septa. Dissepimentarium occasionally with imperfect series of horseshoe dissepiments at tabularium boundary. Tabularium composed of complete or incomplete tabulae, rarely with axial domes of horseshoe section. Increase axial or lateral.

HOLOTYPE. (see de Verneuil & Haime, 1850 : 161). The original of Goldfuss' (1826, pl. 19, fig. 4*a*) illustration of *Cyathophyllum ananas*. Frasnian; Namur, Belgium. This specimen is either mislaid or lost.

MATERIAL. Ramsleigh Quarry: TM(JB)310 (Colony 1), BM(NH) R46370 (Colony 2), TM(JB)306 (Colony 3), BM(NH) R23208 (Colony 4), BM(NH) R46369 (Colony 5), TM(JB)307 (Colony 6), BM(NH) R23217 (Colony 7), BM(NH) R46367 (Colony 8), BM(NH) R46368 (Colony 9), BM(NH) R23302 (Colony 10). Other measured specimens: TM(JB)305B, TM(JB)311–313, TM(JB)318, BM(NH) R46374, BM(NH) R5636, BM(NH) R5642, BM(NH) R5648, BM(NH) R23301, OUM D530–1, OUM D539–41.

South Devon: GSM (Geol. Soc. Coll.) 6183.

DISTRIBUTION. England: Lower Frasnian limestones, Ramsleigh quarry, near Newton Abbot, south Devon. Also Frasnian of Belgium, Germany, Poland and U.S.S.R. (Timan); ? Frasnian of Spain.

DESCRIPTION. The specimens are incomplete colonies frequently comprising more than 200 corallites. Colony shape, size and external features are unknown from the present material but according to Różkowska (1953 : 62) Polish representatives of the species are hemispherical or lenticular colonies up to 7·5 cm. diameter and 3·5 cm. in height, covered basally by a holotheca. Where seen in the English material, the holotheca is about 0·1 mm. thick (Pl. 10, fig. 3). The calices, after Różkowska, are deep with a flat floor, surrounded by an annular rim at the tabularium boundary.

The colonies are massive, pseudocerioid. The corallites, usually pentagonal or hexagonal, are separated from each other by a strong, straight or more frequently zigzagged pseudotheca. Infrequently the pseudotheca may break down in part when the septa are more or less confluent from one corallite to the next.

In the dissepimentarium the septa, major and minor, are usually about 0·05 mm. but may occasionally reach 0·2 mm. in thickness. They are straight and are variably dilated for a short length against the tabularium boundary. The major septa continue as extremely thin processes across the tabularium to the axis where they develop a variable lobate thickening. Usually these septa are fractionally withdrawn from the axis when their dilated ends form a pseudoaulos. The minor septa, normally less dilated than the major, are not continued beyond the thickened portion which may or may not project slightly into the tabularium. The septa are usually smooth sided but may occasionally be lightly carinate.

The dissepiments appear fairly widely spaced in cross-section and are almost always uniserial between adjacent septa. Occasionally the traces of horseshoe dissepiments can be distinguished around the periphery of the tabularium, corresponding to the zone of septal dilatation. The tabularium junction itself is sharply defined.

In longitudinal-section the dissepimentarium is composed of several series of small, well arched dissepiments. The number of series is variable, however, and may rarely be as low as two. Usually the dissepiments are regularly developed with a height of about 0·2 mm. and become somewhat more globose at the boundary with the tabularium. Occasionally, however, the series immediately adjacent to the tabularium may become modified in part to form an incomplete and irregular series of horseshoe dissepiments. The dissepimental surface slopes away from the tabularium for a short distance and is flat lying peripherally.

The tabularium structure is usually simple, varying from complete flat to slightly domed tabulae, to wide slightly arched incomplete vesicular tabulae. The vertical spacing of the plates varies between 0·1 mm. and 0·5 mm. but is usually about 0·2 mm. Occasionally steep sided complete tabulae with narrow flat crests are developed and rarely highly globose vesicles with a horseshoe-shaped section appear in the axis of the tabularium. When two or three of the latter vesicles are superposed, peripheral plates slope steeply downwards and outwards from them.

Increase is axial or lateral, the latter occurring more commonly.

A statistical analysis has been made of specimens of this species from Ramsleigh Quarry. The total sample comprises 25 colonies, 10 of which have been analysed individually. The statistics are given in Table 11 and the data is presented graphically in Text-figs. 16–18.

Discussion. This species was erected by de Verneuil & Haime (1850 : 161) in a fossil list, but as they stated that their new species was *Cyathophyllum ananas* Goldfuss (1826, pl. 19, fig. 4*a*, *non* fig. 4*b*) their designation is valid. *Acervularia goldfussi* was later described in some detail by Edwards & Haime (1851, 1853) and many subsequent workers have mistakenly attributed the species to these authors.

The lectotype of *Acervularia limitata* Edwards & Haime selected by Soshkina (1951 : 97) is lost and the figure of the specimen (Edwards & Haime 1853, pl. 54,

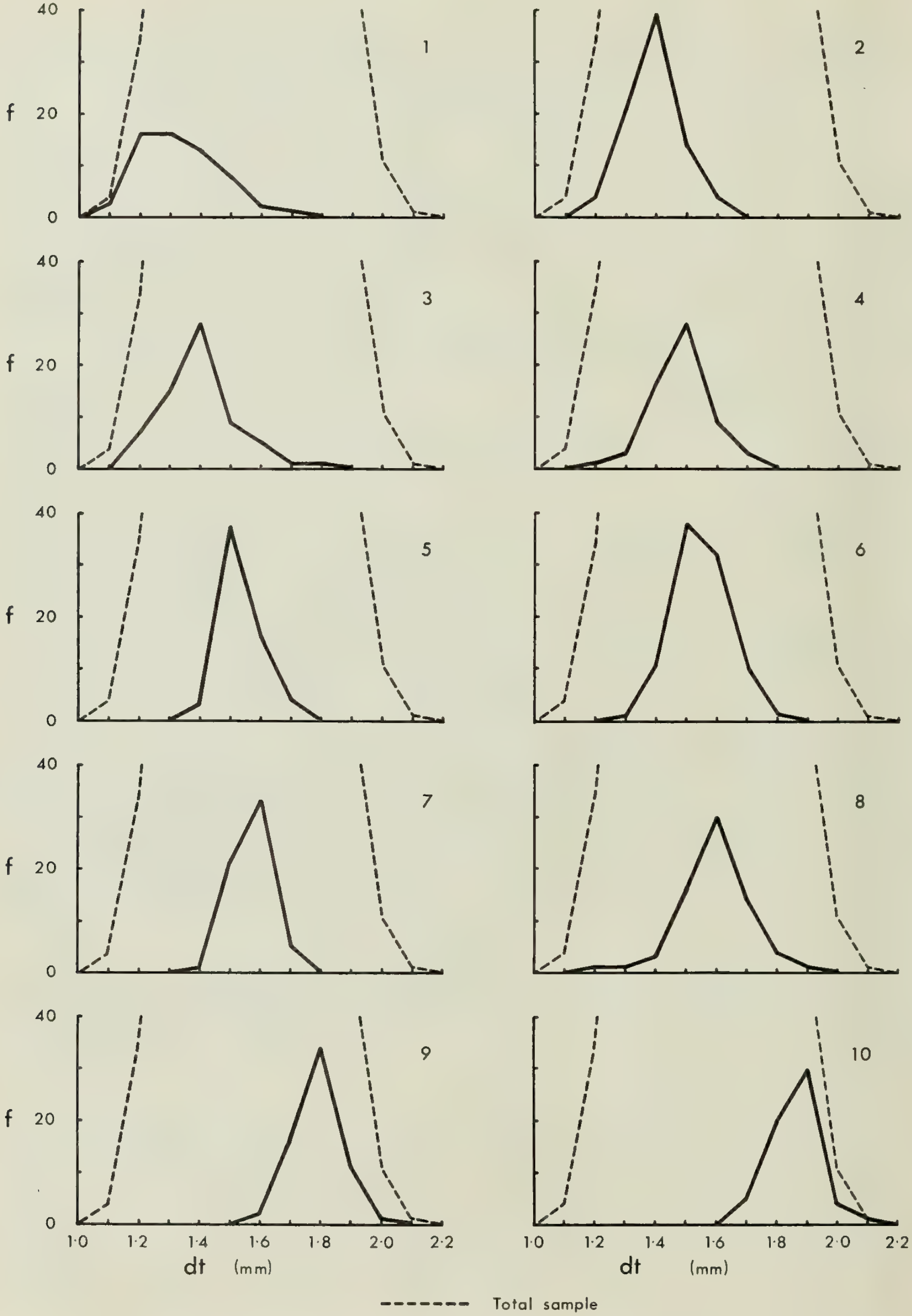
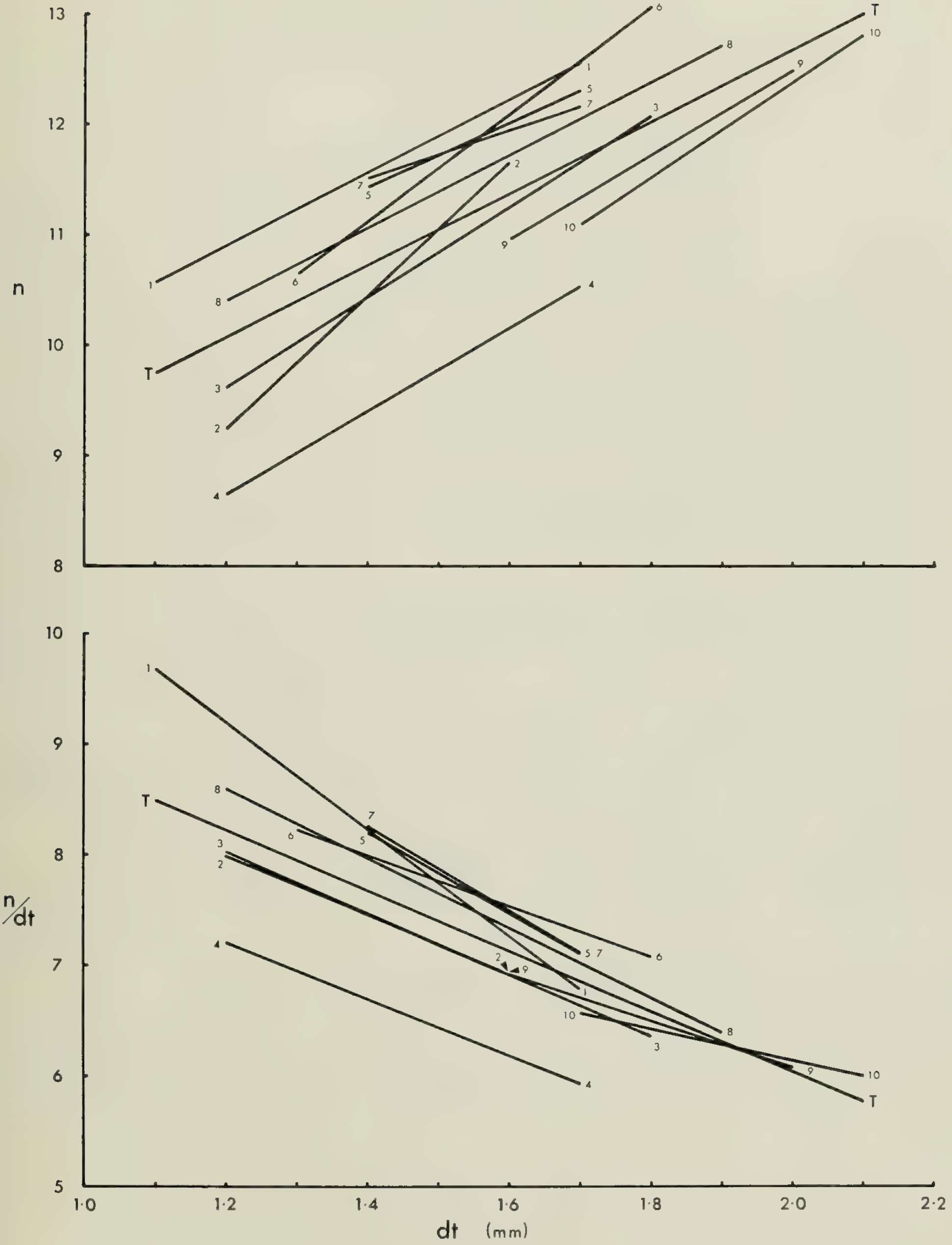


FIG. 17. Tabularium diameter frequency curves for ten colonies of *Frechastraea goldfussi*.



T Total sample

FIG. 18. Graphs of septal insertion and septal-tabularium ratio: tabularium diameter for ten colonies of *Frechastraea goldfussi*.

TABLE 11.—Statistical data for some characters of *Frechastraea goldfussi*.

		Total sample	Colony 1	Colony 2	Colony 3	Colony 4	Colony 5	Colony 6	Colony 7	Colony 8	Colony 9	Colony 10
	N	1,500 (25)	59	82	66	60	60	93	60	70	64	60
dt	**O.R.**	1·1–2·1	1·1–1·7	1·2–1·6	1·2–1·8	1·2–1·7	1·4–1·7	1·3–1·8	1·4–1·7	1·2–1·9	1·6–2·0	1·7–2·1
	$\bar{x}$	1·53	1·33	1·39	1·40	1·48	1·54	1·55	1·57	1·59	1·79	1·86
	s	0·16	0·13	0·091	0·12	0·098	0·069	0·092	0·065	0·12	0·078	0·081
	C.V.	10·10	10·01	6·51	8·75	6·59	4·46	5·92	4·12	7·22	4·35	4·34
	S.E.$_m$	0·0040	0·017	0·010	0·015	0·013	0·0088	0·0095	0·0083	0·014	0·0097	0·010
n	**O.R.**	7–17	9–13	9–13	9–12	8–11	10–13	10–14	11–12	9–12	10–13	10–13
	$\bar{x}$	11·16	11·32	10·40	10·41	9·60	11·82	11·83	11·90	11·70	11·67	11·77
	s	0·51	0·44	0·55	0·50	0·35	0·20	0·44	0·14	0·38	0·30	0·35
	C.V.	4·57	3·89	5·25	4·78	3·60	1·70	3·74	1·19	3·24	2·55	2·93
	S.E.$_m$	0·013	0·057	0·060	0·061	0·045	0·026	0·046	0·018	0·045	0·037	0·045
n/dt	**O.R.**	5·30–9·42	6·47–10·83	6·67–8·57	6·11–9·16	5·29–7·86	6·47–8·57	6·25–8·67	6·88–8·00	6·42–9·17	5·79–7·50	5·72–7·06
	$\bar{x}$	7·32	8·58	7·49	7·49	6·49	7·71	7·67	7·59	7·36	6·53	6·33
	s	0·42	0·64	0·24	0·34	0·25	0·25	0·21	0·25	0·36	0·17	0·12
	C.V.	5·80	7·51	3·22	4·57	3·85	3·27	2·75	3·24	4·92	2·53	1·83
	S.E.$_m$	0·011	0·084	0·027	0·042	0·032	0·033	0·022	0·032	0·043	0·021	0·015
Graphs:—												
n/dt	**r**	0·95	0·63	0·89	0·92	0·90	0·72	0·92	0·78	0·86	0·87	0·94
	a	3·27	3·31	6·03	4·07	3·54	2·93	4·83	2·20	3·30	3·83	4·28
	b	6·14	6·93	2·02	4·73	4·35	7·32	4·36	8·45	6·45	4·83	3·82
n/dt / dt	**r**	—0·97	—0·93	—0·63	—0·92	—0·86	—0·93	—0·87	—0·98	—0·94	—0·85	—0·86
	a	—2·72	—4·84	—2·66	—2·80	—2·56	—3·68	—2·31	—3·81	—3·15	—2·12	—1·44
	b	11·49	15·01	11·19	11·40	10·28	13·36	11·23	13·57	12·38	10·32	9·00

	A	At	At/A
O.R.	0·16–0·27	0·014–0·028	0·073–0·16
$\bar{x}$	0·19	0·019	0·10
s	0·03	0·0034	0·018
C.V.	15·46	17·81	17·74
S.E.$_m$	0·0060	0·00068	0·0036

Graph:—At/A	
r	0·45
a	0·11
b	—0·0029

figs. 1, 1*a*) is of uncertain affinity. The only survivor of the original syntypes of *Acervularia limitata* appears to be the specimen figured by Lonsdale (1840 pl. 58, fig. 1*a*, *non* fig. 1) as *Astrea* (*Favastrea*) *pentagona* which is GSM (Geol. Soc. Coll.) 6183. This specimen is conspecific with *Frechastraea goldfussi*.

Frech (1885 : 49, footnote) considered *Acervularia goldfussi* as interpreted by Edwards & Haime (1851, 1853) to be transitional in form between his *Phillipsastrea ananas* and '*P.*' *pentagona* and accordingly split the former species between the latter two. This explains the apparent inconsistencies in Frech's synonymies. Under *P. ananas* (p. 49) he placed *Cyathophyllum ananas* Goldfuss (1826 pl. 19, figs. 4*a*, *b*) whilst under *P. pentagona* he listed '*Acervularia goldfussi* de Verneuil & Haime 1850 p. 161 *e.p.*'. Frech considered Edwards & Haime's (1853, pl. 53, figs. 3, 3*a*) figured specimen of *Acervularia goldfussi* as conspecific with his *P. pentagona*.

Most subsequent authors appear to have interpreted *F. goldfussi* on Edwards & Haime's figures and descriptions and to have considered it worthy of specific rank, although closely related to *F. pentagona*. In the absence of Goldfuss' type specimen, this interpretation is followed here. The similarity between *F. goldfussi* and *F. pentagona pentagona* is considerable, both being pseudocerioid with essentially straight, non-carinate septa. Differences are confined to small details such as the lobate thickenings on the axial ends of the major septa in *F. goldfussi* and the higher incidence of horseshoe dissepiments in this species. *F. goldfussi* and *F. pentagona pentagona* are, however, clearly differentiated on quantitative characters (Text-fig. 16 and Table 10). The former has a considerably larger tabularium diameter than the latter and the two are significantly different in their growth lines on graphs plotting **n** against **dt** and **At** against **A**. Both differ strongly from *Phillipsastrea ananas* (described on p. 228) through the larger dimensions, the spindle-shaped septa, complex tabularium and row of well developed horseshoe dissepiments of the latter.

Różkowska (1953 : 62 *et seq.*) has described '*Phillipsastraea*' *goldfussi* in detail from the Upper Frasnian of Poland. Her material has a greater range (1·2–2·8 mm.) and a higher mean value (1·8 mm.) for the tabularium diameter than the English representatives. There is no doubt that the two samples are conspecific, however, and the slight size difference may be due to the higher stratigraphical level of the Polish collection.

Attention is drawn for the first time to the rare horseshoe dissepiments developed in representatives of this species. Besides the English examples, Schlüter (1881, pl. 9, fig. 5) illustrated a specimen as *A. pentagona* referable to this species from the Frasnian of Stolberg, near Aachen (Germany) which also clearly shows occasional horseshoes developed against the tabularium junction.

Frechastraea bowerbanki (Edwards & Haime)

Plate 11, Fig. 3; Plate 12, Figs. 1–3

1851 *Smithia bowerbanki* Edwards & Haime : 423.
1852 *Acervularia seriaca* Quenstedt : 664, pl. 60, fig. 3.
1853 *Smithia bowerbanki* Edwards & Haime; Edwards & Haime : 241, pl. 55, figs. 2, 2*a*.
1879 *Acervularia seriaca* Quenstedt; Quenstedt : 536, pl. 163, fig. 1.

1883 *Phillipsastraea bowerbanki* (Edwards & Haime) C. F. Roemer : 391.
1885 *Phillipsastraea bowerbanki* (Edwards & Haime); Frech : 63, pl. 4, figs. 9, 9*a*, *b*.
?1951 *Pachyphyllum bowerbanki* (Edwards & Haime) Soshkina : 89, pl. 16, figs. 1, 2.

But not:
1879 *Smithia bowerbanki* Edwards & Haime; Quenstedt : 536, pl. 162, fig. 39.
1953 *Phillipsastraea bowerbanki* (Edwards & Haime); Różkowska : 67, pl. 8, figs. 3, 4.

DIAGNOSIS. Thamnasterioid *Frechastraea*. Mean tabularium diameter 1·54 mm. with 7 to 12 major septa (East Ogwell sample). Septa rarely slightly dilated at tabularium boundary. Dissepiments characteristically weakly arched and rather elongate; flattened horseshoes extremely rare. Tabularium structure simple.

LECTOTYPE. Selected by Soshkina (1951 : 89). The original of Edwards & Haime's (1853, pl. 55), figs. 2, 2*a*. Devonian; Torquay, south Devon. This specimen appears to be lost.

MATERIAL. Ramsleigh Quarry: TM(JB)294a (Colony 1), TM136/7 (Colony 2). Other measured specimens: BM(NH) R46372–73.

DISTRIBUTION. England: Lower Frasnian limestones, Ramsleigh Quarry, East Ogwell, near Newton Abbot, south Devon. Also Frasnian of Germany (Harz) and ? the U.S.S.R. (southern Urals).

DESCRIPTION. The material is fragmentary and nothing is known of the external features, shape and overall size of the corallum.

The colony is thamnasterioid, with the septa of adjacent corallites most commonly perfectly confluent and less frequently irregularly abutting. Occasional septa may have free ends in the dissepimentarium. The tabularia are regularly and fairly widely spaced.

The septa are 0·05–0·1 mm. thick and are regularly developed between tabularia. They may be straight, but are usually sinuous and occasionally geniculate. In some cases, the sides of the septa are slightly corrugated, presumably by the presence of slightly swollen trabeculae; they are never truly carinate and usually the septa are smooth sided. Septal dilatation at the tabularium boundary is slight or lacking. Usually the major septa project into the tabularium for between 0·1 and 0·2 mm. with no change in thickness. At this point, they thin abruptly and continue towards the axis as strongly attenuate filaments. Occasionally the major septa reach the axis but more commonly, they either curve sharply to become confluent with an adjacent or nearby septum, or they end about a third of the tabularium radius short of the axis. The minor septa end at the tabularium junction.

The dissepiments are uniserial between adjacent septa. The tabularium junction is strongly and sharply defined.

In longitudinal-section, the dissepimentarium is composed of several series of elongate, weakly arched vesicles. The dissepiments are very uniformly developed with a height of 0·1 mm. The surface of the dissepimentarium is flat peripherally, rising slightly to a crest just outside the tabularium junction. Rarely a flattened horseshoe dissepiment may occur among the series forming the crest, whilst on the tabularium side, a vertically discontinuous row of normal dissepiments slopes steeply axially and downwards.

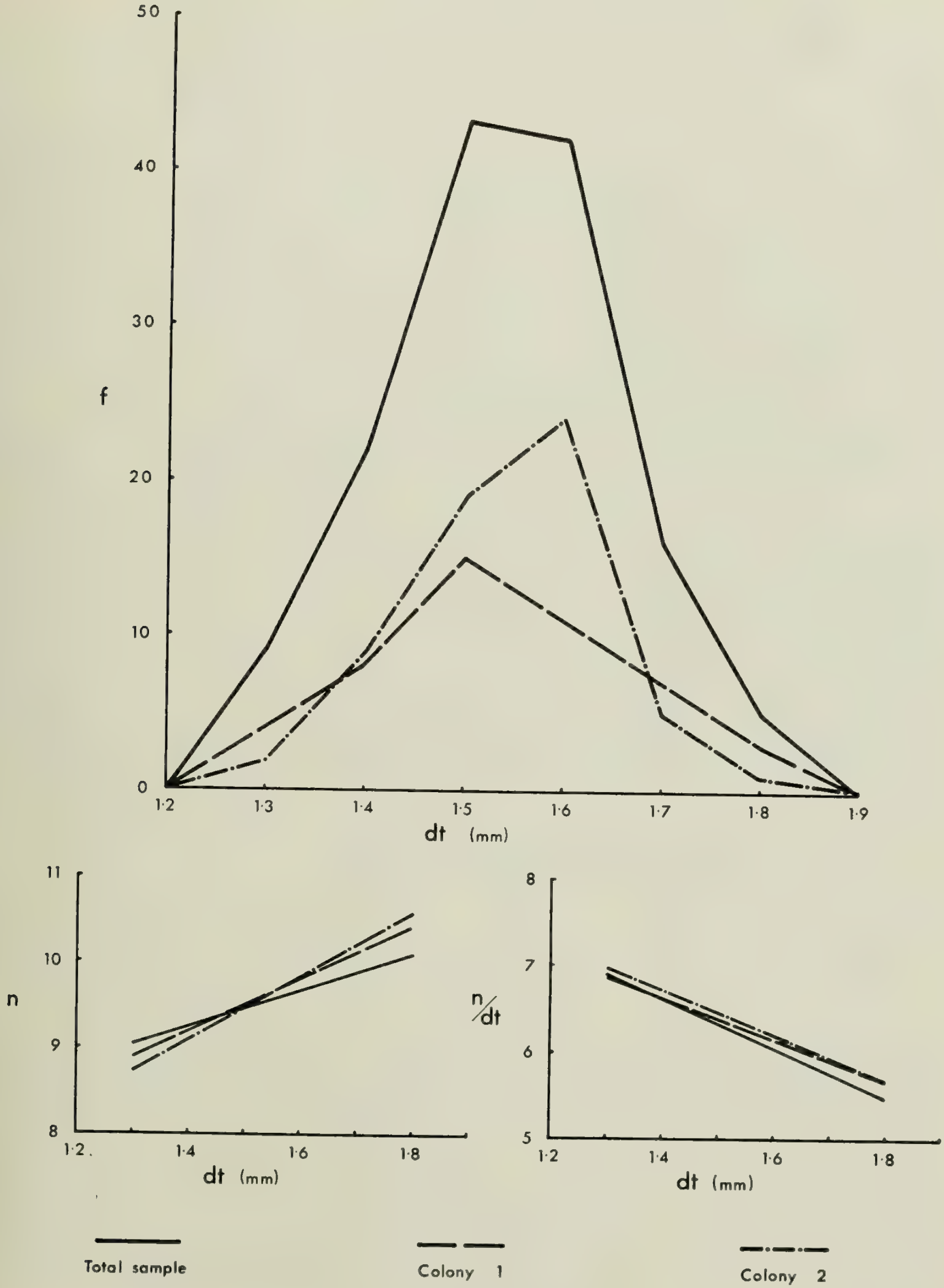


FIG. 19. *Frechastraea bowerbanki.*

TABLE 12.—Statistical data for some characters of *Frechastraea bowerbanki.*

		Total sample	Colony 1	Colony 2
	N	137 (4)	48	60
dt	**O.R.**	1·3–1·8	1·3–1·8	1·3–1·8
	$\bar{x}$	1·54	1·54	1·54
	s	0·12	0·13	0·10
	C.V.	7·73	8·65	6·56
	S.E.$_m$	0·010	0·019	0·013
n	**O.R.**	7–12	8–11	7–12
	$\bar{x}$	9·54	9·65	9·62
	s	0·25	0·42	0·37
	C.V.	2·59	4·31	3·89
	S.E.$_m$	0·021	0·060	0·048
n/dt	**O.R.**	4·71–7·69	5·00–7·14	5·00–7·14
	$\bar{x}$	6·24	6·30	6·36
	s	0·34	0·32	0·26
	C.V.	5·48	5·06	4·09
	S.E.$_m$	0·029	0·046	0·034
Graphs:—				
n/dt	**r**	0·89	0·86	0·86
	a	2·08	3·13	3·70
	b	6·34	4·84	3·91
n/dt / dt	**r**	−0·99	−0·95	−0·77
	a	−2·88	−2·40	−2·57
	b	10·66	9·99	10·32

	A	**At**	**At/A**	Graph:—**At/A**	
O.R.	0·29–0·38	0·016–0·020	0·050–0·057		
$\bar{x}$	0·34	0·018	0·054	**r**	0·96
s	0·043	0·0015	0·0033	**a**	0·036
C.V.	12·56	8·34	6·13	**b**	0·0062
S.E.$_m$	0·021	0·00077	0·0017		

Tabularium structure is simple and is formed with both complete and incomplete tabulae. The complete plates are saucer-shaped, whilst the incomplete plates are flat to slightly arched vesicles, horizontally disposed in the centre of the tabularium and sloping steeply downwards periaxially. The vertical spacing of the tabulae varies considerably between 0·05 and 0·3 mm.

Increase is lateral, with the daughter corallites developing in the dissepimental tissue equidistant from the surrounding adult tabularia.

Only four incomplete colonies from Ramsleigh Quarry were available for analysis, two of which have been selected for individual treatment. The statistics are listed in Table 12 and illustrated graphically in Text-figs. 16 and 19.

DISCUSSION. Although the lectotype is lost, there can be no doubt from Edwards & Haime's (1853 : 241, pl. 55, figs. 2, 2*a*) description and figures, of the interpretation of this species. Figure 2*a* shows clearly the distinctive characters in cross-section which have been described in the present material. Furthermore, they state (1853 : 242) that the diameter of the 'wall' (= tabularium diameter) is about two-thirds of a line, which is approximately 1·4 mm. This agrees with the present observations but contrasts with the measurements given by Różkowska (1953 : 67) for her *Phillipsastraea bowerbanki*. Różkowska's specimen is, in fact, distinct from the present species and belongs to *Frechastraea pentagona minima* (see p. 240).

Quenstedt (1852 : 664, pl. 60, fig. 3) erected a new species, *Acervularia seriaca*, which from his figure and description appears to be conspecific with *F. bowerbanki*. Frech (1885 : 63) was of the same opinion and placed Quenstedt's species in the synonymy for his *Phillipsastrea bowerbanki*. Later Quenstedt (1879 : 536, pl. 163, fig. 1) refigured *Acervularia seriaca* and in the same work (p. 536, pl. 162, fig. 39) also described and figured '*Smithia bowerbanki* Edwards and Haime'. On the evidence of the figures, the specimen of *Acervularia seriaca* appears, as before, to belong to the present species, whilst his *Smithia bowerbanki* is probably referable to *F. pentagona minima*.

F. bowerbanki differs greatly from the species of *Frechastraea* described above. This species has tabularia corresponding in size to those of *F. goldfussi* but the number of septa at any given diameter is strikingly lower in the former. *F. bowerbanki* also occupies a distinctive position on the graph of tabularium area plotted against corallite area, reflecting the relatively wide spacing of the tabularia (Text-fig. 16, Table 10).

F. bowerbanki is further distinguished by its thamnasterioid form and particularly by weakly arched, rather elongate dissepiments in contrast to the globose dissepiments usually found in species of *Frechastraea*.

Genus ***THAMNOPHYLLUM*** Penecke 1894

1894 *Thamnophyllum* Penecke : 563.
1909 *Phacellophyllum* Gürich : 102.
1935 *Disphyllum* {*Phacellophyllum*}; Lang & Smith : 546.
1935 *Thamnophyllum*; Lang & Smith : 563.
1939 *Disphyllum* {*Phacellophyllum*}; Hill : 224.
1939 *Thamnophyllum*; Hill : 227.
partim 1940 *Thamnophyllum*; Hill : 260.
1940 *Phacelophyllum*; Lang, Smith & Thomas : 98.
1940 *Thamnophyllum*; Lang, Smith & Thomas : 133.
1949 *Phacelophyllum*; Stumm : 36.
1949 *Thamnophyllum*; Stumm : 36.
partim 1949 *Macgeea* (*Thamnophyllum*); Schouppé : 100.
1949 *Thamnophyllum*; Soshkina : 77.
partim 1950 *Phacellophyllum* (*Phacellophyllum*); Wang : 219.
1950 *Phacellophyllum* (*Thamnophyllum*); Wang : 219.
1951 *Disphyllum* {*Phacellophyllum*}; Taylor : 185.
1951 *Thamnophyllum*; Soshkina : 74.
1952 *Thamnophyllum*; Soshkina : 85.

1953 *Thamnophyllum*; Różkowska : 13.
partim 1953 *Macgeea*; Różkowska : 18.
1954a *Phacellophyllum*; Hill : 26.
1954 *Thamnophyllum*; Soshkina : 65.
1956 *Thamnophyllum*; Różkowska : 304.
1956a *Macgeea* (*Thamnophyllum*); Flügel : 48.
partim 1956a *Macgeea* (*Macgeea*); Flügel : 53.
1956b *Macgeea* (*Thamnophyllum*); Flügel : 361.
partim 1956b *Macgeea* (*Macgeea*); Flügel : 361.
1956 *Thamnophyllum*; Hill : 281.
1956 *Phacellophyllum*; Hill : 282.
1957 *Thamnophyllum*; Różkowska : 83.
1958 *Macgeea* (*Thamnophyllum*); Flügel : 625.
1958 *Macgeea* (*Thamnophyllum*); Schouppé : 226.
1959 *Thamnophyllum*; Flügel : 115.
partim 1959 *Phacellophyllum*; McLaren : 28.
1960 *Thamnophyllum*; Różkowska : 44.
partim 1963 *Macgeea* (*Macgeea*); Schouppé & Stacul : 288.
1963 *Macgeea* (*Thamnophyllum*); Schouppé & Stacul : 291.
1964 *Thamnophyllum*; Webby : 9.

DIAGNOSIS. Dendroid or phaceloid rugose corals with axial and in one species, lateral increase. Septa of two orders, usually spindle-shaped in dissepimentarium. Dissepimentarium typically with outer series of flat dissepiments and inner series of horseshoe dissepiments. In some species, dissepimental structure obscured by stereoplasmic thickening. Tabulae complete or incomplete, with periaxial plates variably developed.

TYPE SPECIES. Selected by Lang & Smith (1935 : 564) and see Flügel (1958 : 625). *Thamnophyllum stachei* Penecke 1894 : 594, pl. 8, figs. 1–3; pl. 11, figs. 1, 2. Emsian (*barrandei*-Schichten); Marmorbruch am Graz, Austria.

DISTRIBUTION. Lower to Upper Devonian of Europe, Asia, Australia and North America.

DISCUSSION. Penecke (1894 : 563) described four species of *Thamnophyllum*, three of them new and the other *T. trigeminum* (Quenstedt) (see *T. germanicum germanicum* nom. nov., p. 260). From these, Lang & Smith (1935 : 564) selected *T. stachei* as type species and redescribed this and Penecke's other species. They removed *T. trigeminum* from *Thamnophyllum* and assigned it to *Phacellophyllum* Gürich, which they regarded as a genomorph of *Disphyllum*. Gürich (1909 : 102) had placed only '*Phacellophyllum caespitosum* Goldf.' in his new genus. As Lang & Smith (1935 : 547) pointed out, Gürich's figures (1909, pl. 31, figs. 5*a*, *b*) were copied from Schlüter (1881, pl. 9, figs. 6, 7) which fixes the type species of *Phacellophyllum* as *Lithodendron caespitosum* Goldfuss.

Schouppé (1949), in a detailed consideration of species of *Thamnophyllum* and *Phacellophyllum*, was the first to place the latter in synonymy with the former. Furthermore, he made *Thamnophyllum* a subgenus of *Macgeea* on the basis of their similar structural plan, separating *M.* (*Thamnophyllum*) and *M.* (*Macgeea*) principally on their growth form.

Both Soshkina (1951, 1952, 1954) and Różkowska (1953, 1956, 1957, 1960) followed

Schouppé in considering *Phacellophyllum* as synonymous with *Thamnophyllum*, but neither supported the subgeneric relationship with *Macgeea*: Różkowska (1953 : 18, 1957 : 102) listed the characters by which *Macgeea* and *Thamnophyllum* may be distinguished. On the other hand, Hill (1954*a*, 1956) and McLaren (1959) retained *Thamnophyllum* and *Phacellophyllum* as separate genera. McLaren (1959 : 28) pointed out that *T. stachei*, type species of *Thamnophyllum*, is imperfectly known, whereas *Phacellophyllum* has adequately described type material. From Lang & Smith's (1935) descriptions, he regarded the synonymy of the two genera as by no means certain.

The development of periaxial tabulae in the type species of *Phacellophyllum* has led to an involved and lengthy exchange on the taxonomic position of this genus in recent years between Flügel and Schouppé. Flügel (1956*a* : 53, 1965*b* : 361), describing the peripheral plates in the tabularium of *Lithodendron caespitosum* as a third zone of normal dissepiments, compared the structure of the species in longitudinal-section with that developed in typical forms of *Macgeea*. On this basis, he placed *Phacellophyllum* in synonymy with *Macgeea sensu stricto* and retained *Thamnophyllum* as a subgenus of *Macgeea* characterized by only two zones of dissepiments, flat and horseshoe. Schouppé (1958 : 220 *et seq.*) rejected this classification. He considered the ' third dissepimental zone ' to constitute part of the tabularium structure and stated (p. 227) that no sharp line could be drawn between the development of periaxial tabulae in *Macgeea* and *Thamnophyllum*. Schouppé thus retained his 1949 classification, placing *Phacellophyllum* in *Thamnophyllum*, which he separated subgenerically from *Macgeea* on the basis of their contrasting growth form and grade of general structural complexity. Flügel (1959 : 115, footnote) later criticized Schouppé's (1958) subgeneric diagnoses as insufficiently differentiated. Nevertheless, he subscribed to a very similar classification, that of Różkowska (1957), considering not only *Phacellophyllum* to be synonymous with *Thamnophyllum*, but the latter to be generically distinct from *Macgeea*. Finally, Schouppé & Stacul (1963) published a detailed consideration of the genera involved, in which they returned almost exactly to the position held by Flügel (1956). They wrote (1963 : 285) that ' . . . the principal stress in the systematic classification should be laid on the appearance of vesicular elements in the peripheral area of the tabularium. Consequently, all those forms having peripheral vesicles in the tabularium (even if only sporadic . . .) must be placed in *Macgeea* (*Macgeea*). Forms with, on the other hand, simple, peripheral, ' split-open ' tabulae or additional periaxial, sloping, plate-like elements—without peripheral vesicles—belong to *Macgeea* (*Thamnophyllum*).' Thus they placed *Phacellophyllum* in synonymy with *Macgeea* (*Macgeea*).

In the writer's opinion, *Phacellophyllum* is a junior synonym of *Thamnophyllum* and the latter is generically distinct from *Macgeea*. The periaxial elements, so conspicuous in some specimens of *Lithodendron caespitosum* may show considerable variation in their development within the species as a whole (see p. 268). Furthermore, they occur to a greater or lesser degree in many other species of *Thamnophyllum*. It seems unreasonable to suggest a morphological and genetic distinction between the periaxial elements developed in *Phacellophyllum* and *Thamnophyllum* at what must be considered an arbitrary level in their degree of structural complexity. Such a variable character cannot be used as the basis of a subgeneric division, especially as it cuts across the more obvious distinction in growth form. Species of *Macgeea* are simple, conical corals which only rarely show budding. In a collection of 234 individuals belonging to six species and subspecies, Różkowska (1957 : 118) found only four budding specimens. *Thamnophyllum* and *Phacellophyllum*, on the other hand, are phaceloid or dendroid forms with cylindrical corallites. Commonly in *Macgeea*, the horseshoe dissepiments are less regular in form and superposition with a generally more complex tabularium and dissepimentarium structure. In addition, *Macgeea* usually shows distinct bilateral symmetry in the adult stage in contrast to the radial symmetry of *Thamnophyllum* and *Phacellophyllum*.

As McLaren (1959 : 28) remarked, existing knowledge of *T. stachei* is rather imperfect, but the writer believes enough is known from the work of Lang & Smith (1935 : 581) to permit an opinion on the taxonomic status of *Thamnophyllum*. *T. stachei*, from Penecke's figures, Lang & Smith's description and their specimens (BM(NH) R30990–94), shows evidence of all the characteristic features described in better known species of *Thamnophyllum*. As Różkowska (1957 : 101) stated, it is a primitive early member of the genus in which the tabulae are very simple and widely spaced. Stereoplasmic thickening, which in *T. stachei* almost completely obscures the dissepimental structure, is also a variable factor in other species of *Thamnophyllum*.

Thamnophyllum germanicum germanicum nom. nov.

1894 *Thamnophyllum trigeminum* (Quenstedt) Penecke : 596, pl. 8, figs. 4–6.
1959 *Thamnophyllum trigeminum trigeminum* Penecke; Flügel : 117 (see for extensive synonymy).
1960 *Thamnophyllum trigeminum trigeminum* Penecke; Rózkowska : 53.
1963 *Macgeea* (*Thamnophyllum*) *trigemina trigemina* (Penecke) Schouppé & Stacul, text-figs. 5, ?19.
1963 *Macgeea* (*Macgeea*) sp. Schouppé & Stacul, text-fig. 18.

But not:
1879 *Cyathophyllum caespitosum trigemme* Quenstedt : 518, pl. 162, figs. 5–8.

DIAGNOSIS. See Różkowska (1956 : 310).

LECTOTYPE. Selected by Flügel (1959 : 118). UPG 891 (Collections of the Paläontologisches Institut, Graz) labelled by Penecke in 1892 as "*Fascicularia trigemina*". Givetian; (?) Auberg, near Gerolstein, Eifel, Germany.

DESCRIPTION. See Różkowska (1956 : 310).

DISCUSSION. *Cyathophyllum caespitosum trigemme* Quenstedt has been shown by Flügel (1959) to belong to *Favistella* (*Dendrostella*). Hitherto it had been regarded as a species of *Thamnophyllum*, largely due to Penecke (1894 : 596) misinterpreting Quenstedt's description and illustrating as *Thamnophyllum trigeminum* (Quenstedt) a new and generically different species. Subsequent workers had relied mainly on Penecke's work for the identification of Quenstedt's subspecies.

Flügel (1959 : 117) thus described Penecke's material as *Thamnophyllum trigeminum trigeminum* Penecke. The retention of Quenstedt's specific name for Penecke's misidentified material, however, is not in accordance with Article 49 of the I.C.Z.N.

(1964) and a new name is required. With the permission of Professor Flügel, *Thamnophyllum trigeminum trigeminum* Penecke is hereby renamed *Thamnophyllum germanicum germanicum* nom. nov. after the country of origin of Penecke's specimens.

Thamnophyllum germanicum schouppei nom. nov.

Plate 13, figs. 1–4; Plate 14, figs. 1–4

1949 *Macgeea* (*Thamnophyllum*) *caespitosa* (Goldfuss) var. *minus* (F. A. Roemer) Schouppé : 152 *pars*, pl. 10, figs. 21–24; pl. 13, figs. 73–75 (*non* pl. 11, figs. 38–39; pl. 13, figs. 76–77; pl. 14, figs. 100*a*–*c*).
1956*b* *Macgeea* (*Thamnophyllum*) *minima* Schouppé, Flügel : 361.
1965 *Thamnophyllum* cf. *trigeminum* Penecke; Scrutton : 186.

But not:
1855 *Diphyphyllum minus* F. A. Roemer : 29, pl. 6, figs. 12*a*–*c*.

Diagnosis. *Thamnophyllum* with mean corallite diameter 4·2 mm. and 12 to 20 major septa (topotype sample). Axial increase with three or four buds lacking caenogenetic tissue in axils of branches. Tabulae complete or incomplete with periaxial plates sporadically developed. Skeletal elements generally unthickened.

Holotype. See Flügel (1956*b* : 361). UGP327 (Collections of the Paläontologisch Institut, Graz). The specimen is labelled "Middle Devonian, Torquay" only, but it comes without doubt from the Givetian limestones in Dyer's Quarry.

Material. Dyer's Quarry: OUM D506 (Colony 1), OUM D507 (Colony 2), OUM D508 (Colony 3). Other measured material: OUM D271, OUM D509, OUM D511. Additional material: OUM D272, OUM D504–5, OUM D510.

Distribution. Type locality only.

Description. Colonies are phaceloid, up to 100 cm. in diameter, consisting of close-spaced, sub-parallel, cylindrical corallites. External features are unknown as recent weathering has removed the epitheca to expose the peripheral ends of the septa. Calices have not been observed.

In cross-section the corallites are circular to sub-circular. The epitheca, normally about 0·1 mm. thick, is frequently preserved within the matrix. The septa, of two orders, are slightly spindle-shaped in the dissepimentarium. The minor septa may or may not penetrate very slightly into the tabularium but the major septa usually reach a half to two-thirds the distance to the axis. The septa are normally straight in the dissepimentarium but the major septa often become slightly curved or sinuous in the tabularium.

The traces of the sides of the horseshoe dissepiments form a distinctive double wall in cross-section. Between adjacent septa, the two walls are convex towards each other, reflecting the saddle-shaped form of the horseshoe dissepiments. They are, on average, about 0·4 mm. apart, with the outer wall the same distance from the epitheca. The innermost wall is the boundary between the dissepimentarium and the tabularium.

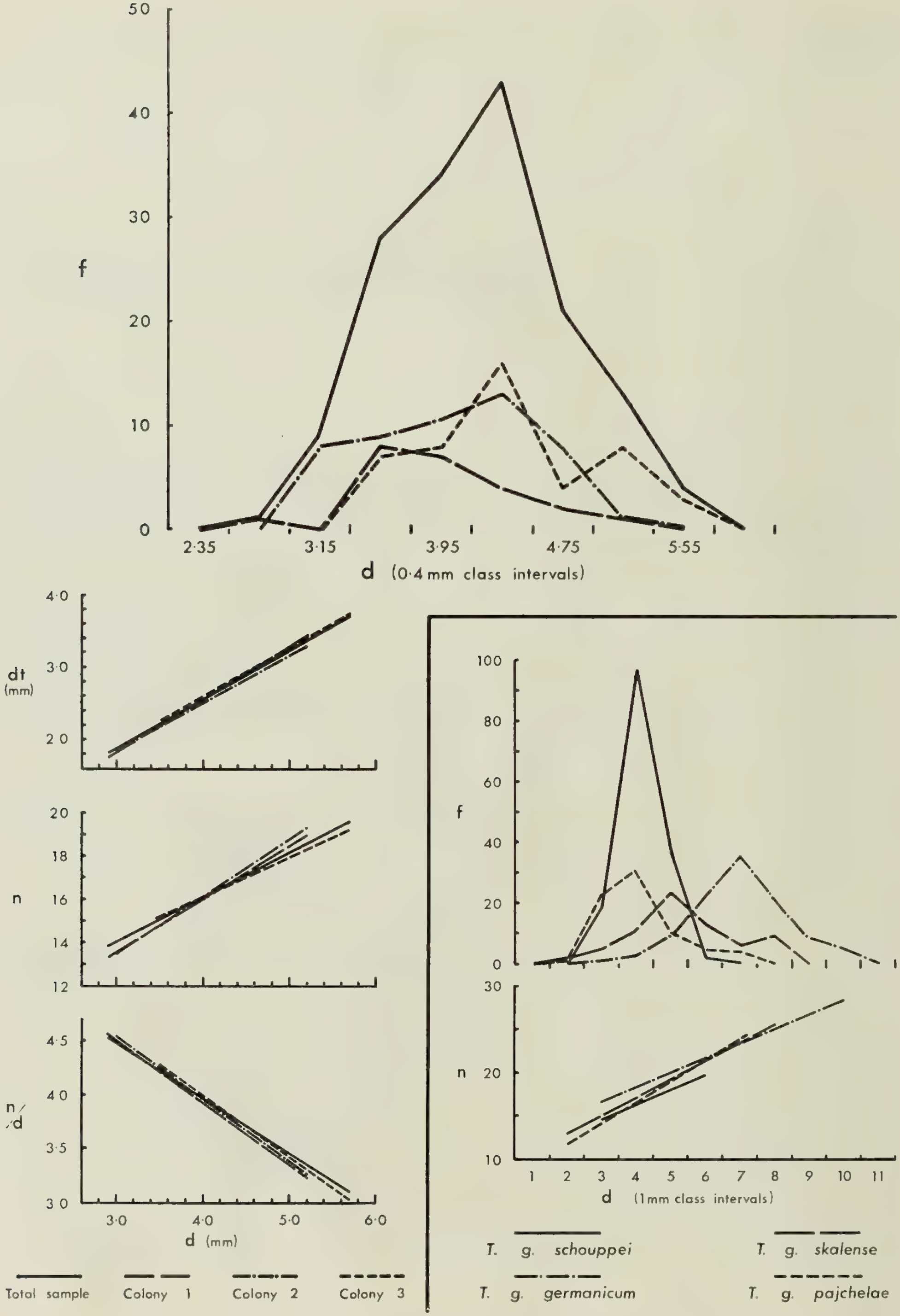


FIG. 20. *Thamnophyllum germanicum schouppei.* Inset: Graphical comparison of some quantitative characters for the subspecies of *Thamnophyllum germanicum.*

In longitudinal-section, the dissepimentarium is composed of an outer series of flat plates and an inner series of horseshoe dissepiments. The outer plates are not always seen as they are easily removed by erosion. They are slightly irregular in spacing, usually between 0·2 and 0·5 mm. apart and always uniserial. They may be perfectly flat, slightly concave or convex. The horseshoe dissepiments are thin walled and regularly developed in a single series, normally between three and four to 1 mm.

The tabulae are complete or incomplete, often with irregularly developed periaxial plates. They may be flat or slightly bowed or arched, and sometimes strongly convex towards the calice. Tabulae in the form of flat-topped domes are rare. The spacing of the tabulae is variable but averages about 18 to 1 cm.

Increase is exclusively axial with three or four daughter corallites produced in each case. There is no indication of extra-dissepimental tissue (caenogenetic tissue of Soshkina 1953) between the newly formed buds. As soon as normal dissepimental tissue begins to form in the axial area of the parent corallite, the daughter corallites become phaceloid.

Increase is often seen in hand specimen but it is difficult to assess quantitatively the frequency with which it occurs. On one specimen, OUM D508/4, three newly formed corallites were seen to bud themselves. The increments of vertical growth between formation and budding in these cases measured 1·3 cm., 1·4 cm. and 1·7 cm. Also the corallite diameters at which budding may occur are usually indeterminate as it is very rare to obtain a cross-section at the inception of blastogeny when it is still possible to measure the diameter of the parent corallite.

A statistical analysis has been made of a total sample comprising six colonies from Dyer's quarry. Three of these colonies have also been analysed individually. The statistics are listed in Table 13 and illustrated graphically in Text-fig. 20.

Discussion. Specimen UPG327 was first described, with some other material, as *Macgeea* (*Thamnophyllum*) *caespitosa* var. *minus* (F. A. Roemer) by Schouppé (1949 : 152). Both Flügel (1965*b* (August) : 361) and Schouppé (1956 (September) : 153, footnote) noted that the Torquay specimen was not in fact conspecific with Roemer's species and Flügel suggested that, as a species in its own right, it should be called *Macgeea* (*Thamnophyllum*) *minima* Schouppé. Under article 49 (Article 70b does not apply here) of the I.C.Z.N. (1964), however, Flügel's use of Roemer's specific name for Schouppé's misidentified material is invalid and a new name is needed. With the permission of Professors A. von Schouppé and H. Flügel, " *Macgeea* (*Thamnophyllum*) *minima* Schouppé " is hereby renamed, as a subspecies of *Thamnophyllum germanicum*, *T. germanicum schouppei* nom. nov.

In his original description, Schouppé (1949 : 155) stated that 'The budding is lateral and not parricidal (= axial) ' in *Macgeea* (*Thamnophyllum*) *caespitosum* var. *minus*. This is certainly true of Roemer's species and Schouppé's remark must have been based on correctly identified material. The holotype, in fact, gives no clear indication of its style of increase, although the evidence from topotypic material of the present subspecies shows that it must be axial.

Thamnophyllum germanicum schouppei is closest in general characteristics to the other subspecies of *T. germanicum* described from the Middle Devonian—*T. ger-*

manicum germanicum nom. nov., *T. germanicum skalense* (Różkowska) and *T. germanicum pajchelae* (Różkowska) (see Różkowska 1960 : 53). As Różkowska (1956) gave data on corallite diameter and number of major septa for the latter three subspecies, it is possible to compare them statistically with the present material

TABLE 13.—Statistical data for some characters of *Thamnophyllum germanicum schouppei.*

		Total sample	Colony 1	Colony 2	Colony 3
	N	153	23	50	46
	O.R.	2·9–5·7	2·9–5·2	3·0–5·2	3·5–5·7
	$\bar{x}$	4·19	3·94	4·00	4·42
d	**s**	0·59	0·51	0·56	0·59
	C.V.	14·08	12·82	13·98	13·35
	S.E.$_m$	0·048	0·11	0·079	0·082
	O.R.	1·7–3·7	1·7–3·3	1·8–3·1	2·1–3·7
	$\bar{x}$	2·69	2·52	2·53	2·84
dt	**s**	0·40	0·37	0·36	0·39
	C.V.	14·79	14·51	14·18	13·80
	S.E.$_m$	0·032	0·076	0·051	0·058
	O.R.	0·55–0·70	0·59–0·70	0·55–0·65	0·62–0·69
	$\bar{x}$	0·64	0·64	0·63	0·65
dt/d	**s**	0·016	0·023	0·020	0·021
	C.V.	2·43	3·63	3·09	3·30
	S.E.$_m$	0·0013	0·0048	0·0028	0·0031
	O.R.	12–20	13–18	12–20	13–20
	$\bar{x}$	16·52	15·91	16·14	16·84
n	**s**	1·22	1·24	1·51	1·09
	C.V.	7·41	7·77	9·35	6·44
	S.E.$_m$	0·099	0·26	0·21	0·16
	O.R.	3·08–5·16	3·41–5·00	3·46–5·16	3·08–4·77
	$\bar{x}$	3·98	4·07	4·06	3·85
n/d	**s**	0·30	0·29	0·31	0·34
	C.V.	7·51	7·00	7·72	8·78
	S.E.$_m$	0·024	0·059	0·044	0·050
Graphs:—					
	r	0·99	0·96	0·98	0·98
dt/d	**a**	0·68	0·73	0·64	0·66
	b	−0·14	−0·34	−0·036	−0·094
	r	0·90	0·85	0·85	0·78
n/d	**a**	2·08	2·45	2·70	1·84
	b	7·83	6·26	5·34	8·71
	r	−0·94	−0·84	−0·78	−0·90
n/d / **d**	**a**	−0·51	−0·56	−0·56	−0·57
	b	6·11	6·29	6·30	6·38

(Table 14 and Text-fig. 20). Only *T. germanicum pajchelae* proved not to be significantly different from *T. germanicum schouppei* in the frequency distribution of their corallite diameters. When septal number was plotted against corallite diameter, however, the lines of all three subspecies were found to be significantly different from that for *T. germanicum schouppei*.

Qualitatively, the latter differs from the other three subspecies by the absence of caenogenetic tissue between newly formed buds. *T. germanicum skalense* also differs through the excessive thickening of its septa in the zone of horseshoe dissepiments and *T. germanicum pajchelae* is remarkable for its regular and widely spaced complete tabulae and general simplification of its internal structure.

T. germanicum schouppei differs markedly from the Frasnian subspecies of *Thamnophyllum germanicum*, *T. germanicum kozlowskii* (Różkowska) and *T. germanicum superius* (Różkowska) (see Różkowska 1960 : 53), through the larger dimensions of the latter pair. The mean corallite diameters of the Frasnian subspecies (Różkowska 1957 : 93 as *T. kozlowskii* and *T. kozlowskii superius*) are 10·03 and 9·28 mm. respectively. In addition, *T. germanicum kozlowskii* is characterized by a more complex dissepimentarium than typical thamnophyllids, with one or two series of horseshoe dissepiments, and the tabularium has highly developed periaxial elements. In the writer's opinion, this form deserves full specific rank. *T. germanicum superius*,

Table 14.—Statistical discrimination between some characters of *Thamnophyllum germanicum* subspecies and *T. germanicum schouppei*. Significant values in bold.

		schouppei	*pajchelae*	*skalense*	*germanicum*
	N	153	73	69	107
	O.R.	3–6	2–7	2–8	3–10
	$\bar{x}$	4·14	4·11	5·36	7·00
d	**s**	0·62	1·13	1·52	1·39
	C.V.	15·01	27·37	28·42	20·81
	S.E.$_m$	0·050	0·13	0·18	0·13
"**t**" test against *schouppei* :—					
	t		0·29	**8·46**	**22·45**
	O.R.	12–20	12–25	10–27	16–29
	$\bar{x}$	16·53	16·90	20·01	23·25
n	**s**	1·06	2·81	3·21	2·34
	C.V.	6·43	16·60	16·04	10·07
	S.E.$_m$	0·086	0·33	0·39	0·23
Graph :—					
	r	0·97	0·99	0·98	1·00
n/d	**a**	1·71	2·49	2·11	1·69
	b	9·45	6·65	8·72	11·43
"**z**" test against *schouppei* :—					
	z (slope)		**13·07**	**6·00**	0·58
	z (position)				**19·07**

described originally as *T. monozonatum* Soshkina by Różkowska (1953 : 14), differs from *T. germanicum schouppei* by the possession of complete, concave tabulae more reminiscent of *T. hornesi* Penecke (as noted by Różkowska) than the *T. germanicum* group.

T. germanicum schouppei is closely similar in most respects to *T. caespitosum* (Goldfuss). The latter, however, has exclusively lateral increase in contrast to the axial increase of the former.

Thamnophyllum caespitosum (Goldfuss) *sensu lato*

Plate 15, figs. 2–4; Plate 16, figs. 1, 2

1826 *Lithodendron caespitosum* Goldfuss : 44, pl. 13, fig. 4.
1848 *Cladocora antiqua* Bronn : 303.
1851 *Lithostrotion antiquum* (Bronn) Edwards & Haime : 439.
1879 *Cyathophyllum caespitosum* Goldfuss; Quenstedt : 509 *pars*.
1881 *Fascicularia caespitosa* (Goldfuss) Schlüter : 103, pl. 9, figs. 6, 7.
1885 *Cyathophyllum caespitosum* Goldfuss; Frech: 33 *pars*.
1909 *Phacellophyllum caespitosum* (Goldfuss) Gürich : 102 *pars*, pl. 31, fig. 5.
1935 *Disphyllum {Phacellophyllum} caespitosum* (Goldfuss) Lang & Smith : 573, *pars*, text-figs. 28, 29, pl. 35, figs. 1, 2.
1949 *Macgeea (Thamnophyllum) caespitosa* (Goldfuss) Schouppé : 138, pl. 9, fig. 3, pl. 11, figs. 40–43.
1949 *Phacelophyllum caespitosum* (Goldfuss); Stumm : 36, pl. 17, figs. 11–13.
1951 *Disphyllum {Phacellophyllum} caespitosum* (Goldfuss); Taylor : 186, pl. 3, figs. 3*a*, *b*, *non* figs. 4*a*, *b*.
1956 *Thamnophyllum caespitosum* (Goldfuss); Różkowska : 308, text-figs. 30–32.
1956*a* *Macgeea (Macgeea) caespitosa* (Goldfuss) Flügel : 54.
1956*b* *Macgeea (Macgeea) caespitosa* (Goldfuss); Flügel : 361.
1957 *Thamnophyllum caespitosum* (Goldfuss); Różkowska : 89, text-fig. 8.
1958 *Macgeea (Thamnophyllum) caespitosum* (Goldfuss); Schouppé : 227, text-figs. 7–9.
1963 *Macgeea (Macgeea) caespitosa* (Goldfuss); Schouppé & Stacul : 268, text-figs. 4, 17.
1964 *Thamnophyllum caespitosum* (Goldfuss); Webby : 9, text-figs. 3*a*–*d*.

But not:
1826 *Cyathophyllum caespitosum* Goldfuss : 60, pl. 19, figs. 2*a*–*d*.
1956 *Phacellophyllum caespitosum* (Goldfuss); Hill : 282, text-fig. 192 (6).

DIAGNOSIS. Phaceloid *Thamnophyllum*. Mean tabularium diameter 6·17 mm. with 18 to 22 major septa (Wolborough Quarry sample). Major and minor septa slightly dilated in zone of horseshoe dissepiments. Dissepimentarium regularly developed with single outer series of horizontal plates and single inner series of horseshoe dissepiments with slightly thickened sides. Tabularium structure highly variable from closely spaced flat-topped domes with inosculating periaxial tabulae to complete, sagging plates, well spaced and with rare subsidiary plates. Increase lateral.

LECTOTYPE (selected by Lang & Smith 1935 : 573). Original of Goldfuss 1826, pl. 13, fig. 4 (Goldfuss Collection, Geologisch-Paläontologisches Institut, Bonn). Givetian; Bensberg, near Köln, Germany.

MATERIAL. BM(NH) R46167–75; middle Givetian limestones, Wolborough Quarry, Newton Abbot, south Devon.

Distribution. England: middle and upper Givetian of the Ilfracombe Beds, north Devon and west Somerset; Givetian limestones, Plymouth; middle Givetian limestones of Wolborough Quarry, Newton Abbot, south Devon. Also common in the Givetian of Europe.

Description. Colonies with well spaced, cylindrical corallites. External features and colony shape unknown as the material is fragmented and embedded in a hard, limestone matrix.

In cross-section, the corallites are circular to sub-circular. The epitheca, which is rarely preserved in the matrix, is about 0·05 mm. thick. Major and minor septa are slightly and evenly dilated to 0·1 mm. thickness for a length of 1–1·25 mm. across the zone of horseshoe dissepiments. The minor septa appear to penetrate slightly into the tabularium whilst the major septa, thin and often slightly sinuous, continue towards the axis. The latter are a half to two-thirds the corallite radius in length.

The traces of the horseshoe dissepiments form two strong internal walls, convex towards each other, in cross-section.

In longitudinal-section, the dissepimentarium comprises an outer series of horizontal plates and an inner series of horseshoe dissepiments, their respective widths in the ratio 1 : 1·3. The plates of the outer series may be flat or very slightly curved and are exclusively uniserial. Their spacing varies between 0·25 mm. and 0·65 mm. The horseshoe dissepiments are also exclusively uniserial and fairly uniform in size and shape. They average 0·3 mm. high. The crest of each horseshoe is thin but the sides are moderately and evenly thickened up to 0·01 mm.

The axial tabulae are complete or incomplete, usually closely spaced and arched with a wide flat crest. Periaxial elements are usually well developed as small arched plates inosculating with the main tabulae. Tabularium structure is, however, very variable and includes corallites with wide flat tabulae with scattered periaxial plates and rarely, well spaced, dominantly complete, saucer-shaped tabulae. The vertical spacing of plates in the axis of the tabularium varies from 14 per cm. when the structure is complex, to 10 per cm. when the structure is simple.

Increase, only observed in a few cases, is lateral with a high angle of divergence between parent and bud.

It was possible to measure only a few corallites accurately so that no attempt has been made to analyse the figures in detail. Data obtained are given in Table 15*b*.

Discussion. See under *Thamnophyllum caespitosum paucitabulatum* (p. 268).

Thamnophyllum caespitosum paucitabulatum subsp. nov.

Plate 15, fig. 1; Plate 16, figs. 3–7; Plate 17, figs. 1–3

Derivation of name. The name, *pauci-* (*paucus* L. = few) *tabulatum*, refers to the simple, relatively wide spaced tabulae characteristic of the subspecies.

Diagnosis. *Thamnophyllum caespitosum* with tabularium composed of flat, slightly arched, or saucer-shaped tabulae with rare periaxial elements. Mean tabularium diameter 5·68 mm. with 16 to 21 major septa (Topotype sample).

HOLOTYPE. BM(NH) R46165; upper Givetian limestones; Lummaton Quarry, Torquay, south Devon.

MATERIAL. BM(NH) R46160–6.

DISTRIBUTION. Type locality only.

DESCRIPTION. Subphaceloid colonies of indeterminate size. Corallites cylindrical, subparallel and fairly well spaced. External features are unknown as the material is embedded in a hard limestone matrix.

The structural details are as for *Thamnophyllum caespitosum* above with the following exceptions and additions.

In longitudinal-section, the tabulae are usually complete. They may be slightly arched with wide flat crests, when small arched periaxial elements are poorly developed. More commonly, the tabulae are flat or saucer-shaped with very rare flat or slightly arched subsidiary plates. There are between 8 and 12 tabulae per cm.; spacing of the plates increases from corallites with arched tabulae to those with saucer-shaped tabulae.

Increase is exclusively lateral, occasionally with two offsets developed at the same level. A small amount of extradissepimental tissue is always developed between the parent and the bud but the angle of divergence is usually high, restricting the plocoid stage to a minimum. Measured corallites showing the early stages of increase are 6·5 and 6·6 mm. in diameter.

A statistical analysis has been made of the sample from Lummaton Quarry. Individual colonies cannot unfortunately be distinguished. The statistics are listed in Table 15*a* and illustrated graphically in Text-fig. 21*a*.

DISCUSSION. Previous descriptions of *Thamnophyllum caespitosum* (Lang & Smith 1935 : 573; Różkowska 1956 : 308; Webby 1964 : 9) all mention tabularia composed of flat or slightly arched tabulae with well developed periaxial elements. No great variation in this structure is mentioned. In fact Flügel (1956*b* : 361) and Schouppé & Stacul (1963 : 268) have placed this species in *Macgeea* on the basis of the complex tabularium structure (see discussion of *Thamnophyllum*, p. 259). The material collected from Wolborough and Lummaton Quarries in south Devon, however, shows considerable variation in the shape and distribution of the tabulae. The sample from Wolborough has a particularly wide range although the majority of the corallites display the tabularium structure considered typical of *T. caespitosum sensu stricto*. At Lummaton, on the other hand, the typical form is not represented and in most cases the tabularia have wide spaced flat or saucer-shaped tabulae with only rare periaxial elements. Although in other respects the two samples are virtually identical, the range in tabularium structure is so striking and, in view of the taxonomic weight hitherto placed on this character, so important that the erection of a new subspecies, *T. caespitosum paucitabulatum*, for the Lummaton material is felt to be justified.

T. caespitosum caespitosum is interpreted strictly in terms of the lectotype (see Lang & Smith 1935 : 573) and includes the material described by Różkowska and Webby. The highly variable middle Givetian Wolborough material, however, is

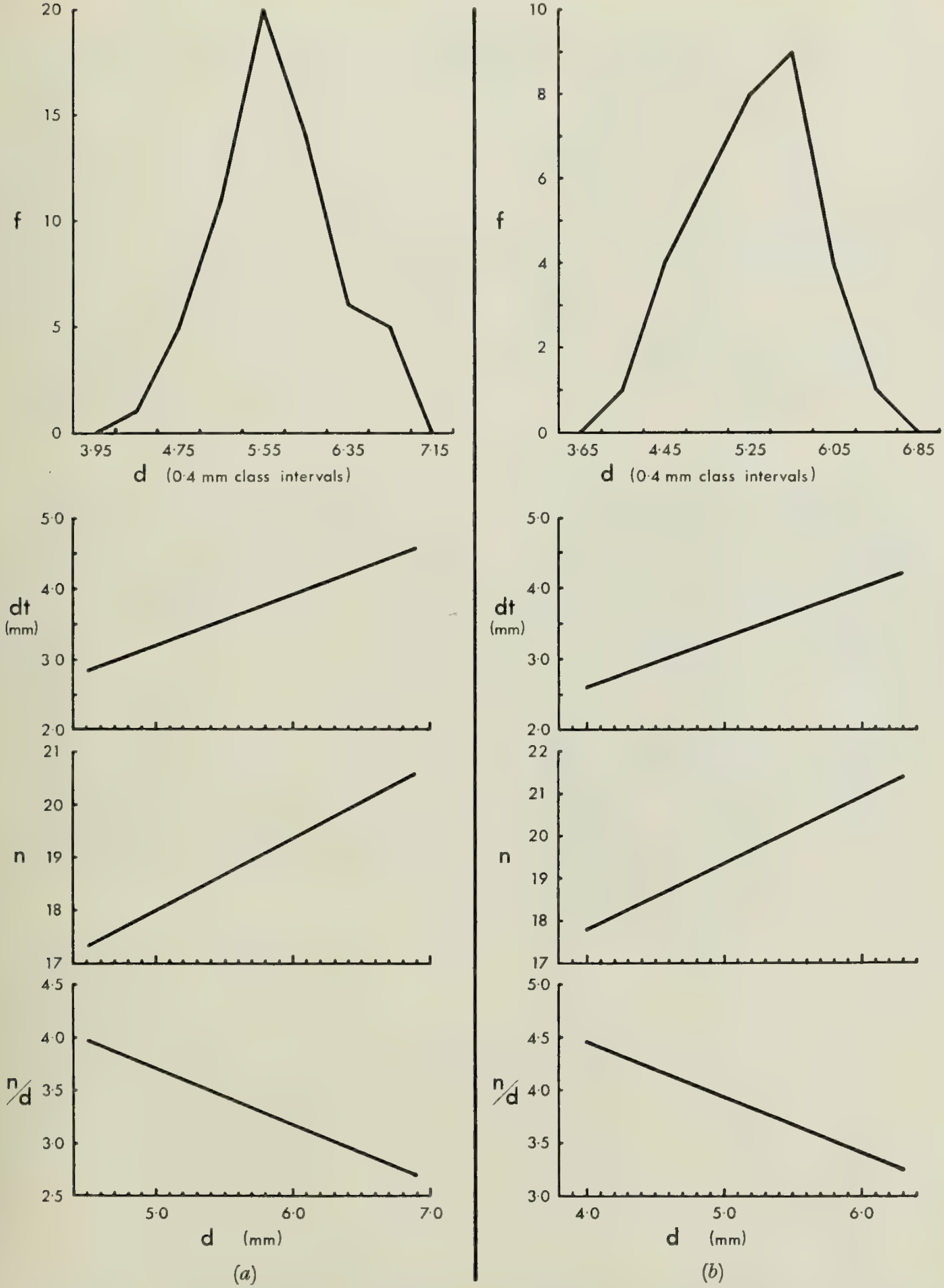


FIG. 21. *a*, *Thamnophyllum caespitosum paucitabulatum*. *b*, *Peneckiella salternensis*.

TABLE 15.—*a.* Statistical data for some characters of *Thamnophyllum caespitosum paucitabulatum. b.* Statistical data for some characters of *Thamnophyllum caespitosum* (*sensu lato*). *c.* Statistical data for some characters of *Peneckiella salternensis.*

		(*a*) Total sample	(*b*) Total sample	(*c*) Total sample
	N	62	12	33
d	**O.R.**	4·5–6·9	5·5–7·2	4·0–6·3
	$\bar{x}$	5·68	6·17	5·28
	s	0·55		0·53
	C.V.	9·66		10·11
	S.E.$_{m}$	0·070		0·093
dt	**O.R.**	3·0–4·9	3·5–4·8	2·7–4·3
	$\bar{x}$	3·70	4·14	3·51
	s	0·40		0·38
	C.V.	10·88		10·87
	S.E.$_{m}$	0·051		0·066
dt/d	**O.R.**	0·62–0·71		0·63–0·68
	$\bar{x}$	0·65		0·67
	s	0·021		0·11
	C.V.	3·27		1·68
	S.E.$_{m}$	0·0027		0·0020
n	**O.R.**	16–21	18–22	17–21
	$\bar{x}$	18·92	20·00	19·91
	s	0·75		0·84
	C.V.	3·95		4·21
	S.E.$_{m}$	0·095		0·15
n/d	**O.R.**	2·61–4·26		4·28–3·33
	$\bar{x}$	3·35	3·26	3·80
	s	0·29		0·28
	C.V.	8·78		7·34
	S.E.$_{m}$	0·037		0·049
Graphs:—				
dt/d	**r**	0·95		0·99
	a	0·73		0·72
	b	−0·47		−0·27
n/d	**r**	0·48		0·81
	a	1·36		1·57
	b	11·19		11·53
n/d / d	**r**	−0·90		−0·94
	a	−0·54		−0·52
	b	6·40		6·55

assigned to *T. caespitosum sensu lato*, from which it is thought the upper Givetian *T. caespitosum paucitabulatum* from Lummaton directly descended.

Quantitatively, *T. caespitosum paucitabulatum* has a slightly lower mean corallite diameter than that for *T. caespitosum sensu lato* although the latter has insufficient measurements for accurate comparison (Tables 15*a*, *b*). Figures available for *T. caespitosum caespitosum*—' close to 6 mm. ' corallite diameter with ' usually 18 to 19 ' major septa (Webby 1963 : 10) and ' corallites average about 6 mm. in diameter and have about 20 major septa ' (Różkowska 1956 : 308)—compare closely with those for the Wolborough material. Lang & Smith (1953 : 574), however, record fewer major septa—16 to 18—with an average corallite diameter of 6 cm. (*sic*) in the lectotype of *T. caespitosum caespitosum*.

T. caespitosum is structurally most similar to the *T. germanicum* group but is distinguished from it, and all other species of *Thamnophyllum*, by the possession of lateral budding.

Thamnophyllum spp.

MATERIAL. BM(NH) R46181, middle Givetian limestones (see Middleton 1959), Shinner's Bridge Quarry, near Dartington (SX 78906225); BM(NH) R46178, Givetian limestones, road cutting immediately south of junction of Babbacombe Road with Acre Lane, Torquay (SX 93186477); BM(NH) R46177, Givetian limestones, disused quarry on Teignmouth Road, Torquay (SX 91126553); BM(NH) R46179–80, Middle Devonian (?Givetian) thin bedded limestones, 80 ft. above sea level in cliff at northern end of Redgate Beach, Torquay (SX 93516494). All south Devon.

DISCUSSION. These fragments, which do not all belong to the same species or subspecies, can nevertheless be placed in either *Thamnophyllum caespitosum* or *T. germanicum*. Unfortunately none of them gives evidence of the mode of increase which is critical in distinguishing between the two species. Further material may eventually enable the accurate determination of these specimens.

Genus ***PENECKIELLA*** Soshkina 1939

partim 1939 *Peneckiella* Soshkina : 23.
partim 1939 *Disphyllum*; Hill : 224.
partim 1949 *Peneckiella*; Soshkina : 141.
partim 1949 *Macgeea* (*Thamnophyllum*); Schouppé : 115.
partim 1950 *Phacellophyllum* (*Phacellophyllum*); Wang : 219.
partim 1951 *Peneckiella*; Soshkina : 103.
partim 1952 *Peneckiella*; Soshkina : 103.
partim 1954 *Peneckiella*; Soshkina : 32.
partim 1954a *Peneckiella*; Hill : 25.
1956 *Peneckiella*; Schouppé : 153.
1956a *Peneckiella*; Flügel : 55.
1956b *Peneckiella*; Flügel : 355.
partim 1956 *Peneckiella*; Hill : 282.
1958 *Peneckiella*; Schouppé : 229.
1959 *Acinophyllum* McLaren : 22.

partim 1959 *Phacellophyllum*; McLaren : 28.
1960 *Peneckiella*; Różkowska : 29.
1960 *Sudetia* Różkowska : 35.
partim 1965 *Peneckiella*; Strusz : 555.

DIAGNOSIS. Phaceloid or dendroid rugose corals. Septa, major and minor, may be lightly carinate and dilated in dissepimentarium. Characterized by one or two, seldom more, series of dissepiments of variable form but always including peneckielloid dissepiments. Horseshoe, flat and sigmoidal dissepiments may also be present. Tabulae complete or incomplete, frequently with flat-topped domes. Increase usually lateral but may be axial.

TYPE SPECIES. *Diphyphyllum minus* F. A. Roemer (1855 : 29, pl. 6, figs. 12*a–c*). Frasnian, Ibergerkalk; Winterberg near Bad Grund, Harz, Germany.

DISTRIBUTION. Uppermost Givetian and Frasnian of Europe; ?upper Lower Devonian to Frasnian of Australia; ?Lower, Middle and Upper Devonian of North America.

DISCUSSION. In her original diagnosis, Soshkina (1939 : 23) included ' simple or composite, fasciculate and massive ' corals and described the dissepimentarium as composed of ' one row of regularly spaced vesicles . . . sometimes flattened from above '. Soshkina (1954 : 32) later gave a slightly different diagnosis for the genus which Flügel (1956*b* : 355) mistranslated as excluding massive forms from *Peneckiella*. Schouppé (1958 : 191) pointed out Flügel's mistake but himself concluded that *Peneckiella* should be correctly defined (1958 : 192) as excluding massive forms. Both Flügel (1956*b*) and Schouppé (1958) gave extended discussions of this genus and concluded that it is characterised basically by a single, rarely double row of horseshoe dissepiments only in the dissepimentarium.

It is clear, however, from the holotype of *Peneckiella minor*, type species of *Peneckiella*, that it is peneckielloid (see Różkowska 1960 : 32) and not true horseshoe dissepiments that are characteristic of the genus. No true horseshoe dissepiments can be positively identified in the holotype (Plate 17, figs. 4, 5), although they do occur in a subsidiary role in the dissepimentaria of some topotype specimens.

McLaren (1959 : 22) in the discussion of his new genus *Acinophyllum*, remarked that, from Frech's (1885 : 34, pl. 1, figs. 3, 3*a*, 3*b*) account of *Cyathophyllum minus* (F. A. Roemer), which was based on Roemer's specimen, ' it would appear likely that *Acinophyllum simcoense* is congeneric with *Diphyphyllum minus* and therefore with *Peneckiella*. But *D. minus* has been described several times since Frech and on no occasion has the description agreed closely with his. ' In fact Frech's drawing (pl. 1, fig. 3*a*) more accurately portrayed the dissepimental structure of *D. minus* (except for the divergence of the septal trabeculae) than either Flügel's (1956*b*, text-fig. 1*c*) or Schouppé's (1958, text-figs. 13, 14) illustrations.

Dr. W. A. Oliver Jr. has kindly sent the writer two small fragments (BM(NH) R463661/–2) from a large colony of *Acinophyllum simcoense* from the Bois Blanc Formation (south quarry, Haldimand Quarries and Construction Ltd., north east of Hagarsville, Ontario). Slides cut from this material show well developed peneckielloid dissepiments in longitudinal-section extremely similar to those of *P. minor*.

Where subsidiary dissepiments are developed, however, these are normal globose vesicles; no horseshoe dissepiments have been seen. The septal carination in cross-section is very variable and smooth septa do occur. Certainly the presence or absence of carinae cannot be considered to be of great significance here at the generic level. On all other characters, the specimen of *A. simcoense* can be placed with little doubt in *Peneckiella* and *Acinophyllum* is thus considered a junior synonym of that genus.

Różkowska (1960 : 35) erected a new genus and species, *Sudetia lateseptata* which she considered (1960 : 50) to be a direct phylogenetic descendant of, and closely related to *Peneckiella*. The author is of the same opinion but believes that *Sudetia* does not warrant separate generic status.

Peneckiella, as suggested by Różkowska (1960), apparently evolved from *Thamnophyllum*, chiefly by the fusion and modification of the horseshoe and flat dissepiments characteristic of the latter, leading to the diversification of dissepimental types found in *Peneckiella*. Besides the characteristic peneckielloid dissepiments, forms such as *P. minor kunthi* (Dames) (see Różkowska 1960, text-fig. 27), *P. mesa* (Hill) (see Strusz 1965, text-fig. 156) and *P. salternensis* sp. nov. (see p. 274), include varying proportions of horseshoe, flat and sigmoidal dissepiments in their dissepimentaria. In fact, a morphological series can apparently be traced from a horseshoe and flat dissepimental pair, through sigmoidal to peneckielloid dissepiments. *P. minor sensu stricto*, with a fairly uniform peneckielloid dissepimentarium and only rare horseshoe dissepiments would appear to be an advanced form and *P. lateseptata*, as suggested by Różkowska, a late stage form in this evolutionary trend.

Peneckiella salternensis sp. nov.

Plate 18, figs. 1–4

1965 *Peneckiella* cf. *minor* (Roemer); Scrutton: 188, text-fig. 1.

DERIVATION OF NAME. After the type locality in Saltern Cove.

DIAGNOSIS. Phaceloid *Peneckiella*. Mean tabularium diameter 3·51 mm., mean corallite diameter 5·28 mm. with 17 to 21 major septa (topotype sample). Septa slightly and variably dilated; may be weakly carinate. Dissepimentarium dominated by peneckielloid dissepiments, but with horseshoe, flat and sigmoidal dissepiments also present. Tabulae regularly developed in form of wide, flat-topped domes. Increase lateral.

HOLOTYPE. OUM D548. Frasnian; thick bedded limestone immediately above igneous rock; southern end of Saltern Cove (SX 89505842), near Paignton, south Devon.

MATERIAL. Saltern Cove (main *Peneckiella* horizon); measured material: OUM D501, OUM D546–48, OUM D550–51, OUM D553; additional material: OUM D549, OUM D552. Saltern Cove (thin bedded limestones): OUM D554.

DISTRIBUTION. Frasnian; type horizon (main *Peneckiella* horizon) and from thin bedded limestones in the sequence immediately above, southern end of Saltern Cove, south Devon.

Description. Colonies are phaceloid with circular to sub-circular, close spaced corallites. External features are unknown as the specimens are preserved in a tough matrix. The epitheca is 0·1 mm. or slightly less in thickness.

The major and minor septa are variably dilated in the dissepimentarium, occasionally strongly spindle-shaped but showing all gradations to a virtually unthickened state. Their thickness ranges from about 0·3 mm. to 0·1 mm. or slightly less. The septa may be straight or zigzagged in this zone, and are sometimes variably carinate. Carinae are yardarm on straight septa and xyloid on zigzagged septa.

Minor septa end at the tabularium junction but the major septa, slightly attenuated, continue into the tabularium with a thickness of about 0·05 mm. or less. The major septa may be straight to slightly sinuous in the tabularium and normally extend about half way to the axis. Septal length is somewhat variable, however, and rarely they may more or less reach the axis or, conversely, only just penetrate into the tabularium. The axial ends of the major septa may rarely be slightly thickened.

The traces of one or two rows of dissepiments, uniserial between adjacent septa, may be seen in cross-section. The tabularium junction can be easily distinguished but it is not usually strongly defined.

In longitudinal-section, the dissepimentarium is composed of one or two series of highly variable dissepiments. The peneckielloid form dominates when the dissepimentarium is usually but not always uniserial. The occurrence of horseshoe dissepiments may be accompanied by peripheral flat dissepiments but normally the latter are very rare; horseshoes always occur in the inner row of biserial parts of the dissepimentarium. Sigmoidal dissepiments occur with about the same frequency as horseshoe dissepiments. The ratio of peneckielloid dissepiments to horseshoe dissepiments is highly variable from corallite to corallite, ranging between extremes of 2 : 1 and 10 : 1. The various dissepimental types are randomly distributed up the length of the corallites and the vertical spacing of the dissepiments may vary from 0·1 to 0·5 mm.

Tabularium structure is very constant, consisting of regularly and closely spaced, wide, flat-topped domes. Periaxial tabulae in the form of steeply dipping peripheral vesicles may sometimes occur. There are about 40 tabulae in 1 cm.

Increase is lateral corresponding closely to the ‘ thamnophylloid lateral ’ type described by Różkowska (1960 : 31). The diameters of parent corallites displaying increase range from 5·3 to 5·6 mm.

A statistical analysis of the Saltern Cove material has been made but unfortunately individual colonies could not be distinguished. The statistics are listed in Table 15*c* and illustrated graphically in Text-fig. 21*b*.

Discussion. *Peneckiella salternensis* can be distinguished from *P. lateseptata* (Różkowska), *P. nalivkini* Soshkina and *P. achanaiensis* Soshkina on dissepimental character alone. The latter three are all characterized by almost exclusively uniserial dissepimentaria of uniformly developed peneckielloid dissepiments. *P. minor minor* (Roemer) apparently has a somewhat less regular dissepimentarium, with the presence of occasional horseshoes. The tabularium, however, although sometimes developing dome-shaped plates, shows tabulae irregularly developed and frequently depressed in the axial area. This is in strong contrast to the regularly developed dome-shaped tabulae characteristic of *P. salternensis*. In addition, data given by Flügel (1956*b* : 359) for *P. minor minor* (Table 16) shows that subspecies to be smaller, with fewer septa than *P. salternensis*.

P. minor kunthi (Dames), *P. mesa* (Hill) and *P. boreensis* Strusz have dissepimentaria of similar complexity to *P. salternensis*. *P. minor kunthi*, however, has flat, or more commonly, incomplete, axially depressed tabulae and is smaller (Table 16) than *P. salternensis*. *P. mesa* and *P. boreensis* have flat-topped domes in their tabularia, but both Australian species have axial increase in contrast to the lateral increase in *P. salternensis*. In addition, *P. salternensis* is larger than *P. mesa* and *P. boreensis* (see Table 16) and the latter is further distinguished by excessive dilatation of the septa in the dissepimentarium.

Table 16.—Quantitative comparison of some species and subspecies of *Penechiella*.

			d	dt	n
P. salternensis		O.R.	4·0–6·3	2·7–4·3	17–21
Paignton, S. Devon,		$\bar{x}$	5·28	3·51	19·91
England.					
P. minor minor		O.R.	3·5–4·9	2·9–3·9	15–18
Harz, Germany.	1	$\bar{x}$	3·9		
P. minor minor		O.R.	3·5–5·6	2·9–4·2	14–18
Antitaurus, Turkey.	1	$\bar{x}$	4·8		
P. minor kunthi		O.R.	2·5–4·8		12–18
Mokrzeszów, Poland.	2	$\bar{x}$			
P. mesa		O.R.	1·4–8·4	1·0–3·9	11–23
Wellington, N.S.W.,		$\bar{x}$	3·6	2·12	17·00
Australia.	3				
P. boreensis		O.R.	0·9–10·1	0·7–6·5	3–28
Molong, N.S.W.,		$\bar{x}$	4·5	2·8	16·00
Australia.	3				

Data from 1 Flügel, 1956b: 359.
2 Różkowska, 1960: 29.
3 Strusz, 1965: 557, 562.

Unfortunately data given for other species and subspecies of *Penechiella* are not in a form allowing statistical comparison with the present material. Nevertheless they afford a valuable general indication of quantitative relationships and are therefore listed in Table 16.

REFERENCES

Blainville, H. M. D. de 1834. *Manuel d'Actinologie ou de Zoophytologie.* viii + 695 pp. Atlas. Paris.

Bronn, H. G. 1848–9 *Index Palaeontologicus.* **1** (1), lxxxiv + 1–775 (1848); **1** (2), 777–1381 + [1] (1848); **2**, 1–980 (1849). Stuttgart.

BULVANKER, E. Z. 1958. *Devonskie chetyrekhluchevye korally okrain Kuznetskogo basseyna.* 212, pp. 93 pls. VSEGEI, Leningrad. [In Russian].

CHILINGAR, G. V. 1956. Review: About dynamics of septal development in tetracorals during ontogeny, by K. G. Voynovskiy-Kriger. *J. Paleont.*, Chicago, **30** : 406–411, 9 text-figs.

DANA, J. D. 1846. Genera of fossil corals of the family Cyathophyllidae. *Am. J. Sci. Arts.*, New Haven (2), **1** : 178–189, text-figs. 1–5.

DINELEY, D. L. 1961. The Devonian system in South Devonshire. *Fld. Stud.*, London, **1** : 121–140, 6 text-figs.

DINELEY, D. L. & RHODES, F. H. T. 1956. Conodont horizons in the west and south-west of England. *Geol. Mag.*, London, **93** : 242–248, text-figs. 1–5.

EDWARDS, H. M. & HAIME, J. 1850. A Monograph of the British Fossil Corals, Part 1. Introduction, etc. : i–lxxxv + 1–71, pls. 1–11. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1851. Monographie des Polypiers fossiles des Terrains palaeozoïques. *Arch. Mus. natn. Hist. nat. Paris*, **5** : 1–501, pls. 1–20.

—— 1852. A Monograph of the British Fossil Corals, Part 3. Corals from the Permian Formation and the Mountain Limestone : 147–210, pls. 31–46. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1853. A Monograph of the British Fossil Corals, Part 4. Corals from the Devonian Formation : 211–244, pls. 47–56. *Palaeontogr. Soc.* [*Monogr.*], London.

—— 1855. A Monograph of the British Fossil Corals, Part 5. Corals from the Silurian Formation : 245–299, pls. 57–72. *Palaeontogr. Soc.* [*Monogr.*], London.

EHLERS, G. M. & STUMM, E. C. 1953. Species of the Tetracoral genus *Billingsastraea* from the Middle Devonian of New York and other regions. *Bull. Buffalo Soc. nat. Sci.*, **21** : 1–11, pls. 1–6.

ELLIOTT, G. F. 1961. A new British Devonian alga, *Palaeoporella lummatonensis*, and the brachiopod evidence of the age of the Lummaton Shell-Bed. *Proc. Geol. Ass.*, London, **72** : 251–260, pls. 9, 10.

ETHERIDGE, R. 1899. Descriptions of new or little known Victorian Palaeozoic or Mesozoic fossils, No. 1. *Prog. Rept. geol. Surv. Vict.*, Melbourne, **11** : 30–36, pls. A, B.

FLEMING, J. 1828. *A History of British Animals.* xxiii + 565 pp. Edinburgh.

FLÜGEL, H. 1956*a*, Die " Sandsteinfazies " des Mitteldevons von Graz. *Sber. Akad. Wiss. Wien, math.-nat. Kl.*, 1956 : 45–57, 2 tables.

—— 1956*b*. Kritische Bemerkungen zum Genus *Peneckiella* Soshkina. *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, 1956, 8 : 355–365, 3 text-figs.

—— 1958. Korallen und Stromatoporen aus den Geröllen der Karbonkonglomerate des Ljubljana-Feldes. *Razpr. Slov. Akad. Znan. Umet.*, Ljubljana (4), **4** : 623–629, text-fig. 1.

—— 1959. Zur Kenntnis der Typen von *Favistella* (*Dendrostella*) *trigemme trigemme* (Quenst., 1881) und *Thamnophyllum trigeminum trigeminum* Penecke 1894. *Neues Jb. Geol. Paläont. Mh.*, Stuttgart, 1959, 3 : 113–120.

FONTAINE, H. 1961. Les Madréporaires paléozoïques du Viêt-Nam, du Laos et du Cambodge. *Archs géol. Viêt-Nam*, Saigon, **5** : 1–276. Atlas, pls. 1–35.

—— 1964. Madréporaires paléozoïques du Viêt-Nam, du Cambodge, du Laos et du Yunnan. Nouvelles déterminations et notes bibliographiques. *Archs géol. Viêt-Nam*, Saigon, **6** : 75–92, pl. 8.

FRECH, F. 1885. Die Korallenfauna des Oberdevons in Deutschland. *Z. dt. geol. Ges.*, Berlin, **37** : 21–130, pls. 1–11.

GLINSKI, A. 1955. Cerioide Columnariidae (Tetracoralla) aus dem Eifelium der Eifel und des Bergischen Landes. *Senckenberg. leth.*, Frankfurt a.M., **36** : 73–114, pls. 1, 2.

GOLDFUSS, G. A. 1826–33. *Petrefacta Germaniae*, **1** : 1–76, pls. 1–25 (1826); 77–164, pls. 26–50 (1829); 165–240, pls. 51–71 (1831); 241–252 (1833). Düsseldorf.

GÜRICH, G. 1896. Das Palaeozoicum des Polnischen Mittelgebirges. *Verhandl. Russ.-kais. Min. Ges. St. Petersb.* (2) **32** : vi + 1–539, pls. 1–15.

—— 1909. *Leitfossilien*, **2.** *Devon* : 97–199, pls. 29–52. Berlin.

HILL, D. 1935. British terminology for rugose corals. *Geol. Mag.*, London, **72** : 481–519, 21 text-figs.

—— 1939. The Devonian Rugose Corals of Lilydale and Loyola, Victoria. *Proc. R. Soc. Vict.*, Melbourne (n.s.) **51**, 2 : 219–256, pls. 13–16.

—— 1940. The Lower Middle Devonian Rugose Corals of the Murrumbidgee and Goodradigbee Rivers, N.S.W. *J. Proc. R. Soc. N.S.W.*, Sydney, **74** : 247–276, pls. 9–11.

—— 1942*a*. The Lower Devonian Rugose Corals from the Mt. Etna Limestone, Qld. *Proc. R. Soc. Qd.*, Brisbane, **54** : 13–22, pl. 1.

—— 1942*b*. The Devonian Rugose Corals of the Tamworth District, N.S.W. *J. Proc. R. Soc. N.S.W.*, Sydney, **76** : 142–164, pls. 2–4.

—— 1942*c*. Middle Palaeozoic Rugose Corals from the Wellington District, N.S.W. *J. Proc. R. Soc. N.S.W.*, Sydney, **76** : 182–189, pls. 5, 6.

—— 1954*a*. Coral Faunas from the Silurian of New South Wales and the Devonian of Western Australia. *Bull. Bur. Miner. Resour. Geol. Geophys. Aust.*, Melbourne, **23** : 1–51, pls. 1–4.

—— 1954*b*. Devonian Corals from Waratah Bay, Victoria. *Proc. R. Soc. Vict.*, Melbourne, (n.s.), **66** : 105–118, pls. 6–9.

—— 1956. *Rugosa*. *In* MOORE, R. C. (Ed.) *Treatise on Invertebrate Paleontology*, **F** : 233–324, text-figs. 165–219. Lawrence, Kansas.

HOUSE, M. R. 1963. Devonian ammonoid successions and facies in Devon and Cornwall. *Q. Jl geol. Soc. Lond.*, **119** : 1–27, pls. 1–4.

HOUSE, M. R. & SELWOOD, E. B. 1965. *Palaeozoic palaeontology in Devon and Cornwall. In* HOSKING, K. F. G. & SHRIMPTON, G. J. (Eds.) *Present views of some aspects of the geology of Cornwall and Devon* : 45–86, pls. 1–4. Penzance.

IMBRIE, J. 1956. Biometrical methods in the study of Invertebrate fossils. *Bull. Am. Mus. nat. Hist.*, New York, **108** : 211–252, 10 text-figs.

International Code of Zoological Nomenclature. 1964. xx + 176 pp. London.

JUKES-BROWNE, A. J. 1906. The Devonian Limestones of Lummaton Hill, near Torquay. *Proc. Geol. Ass.*, London, **19** : 291–302, 1 text-fig.

KATO, M. 1963. Fine skeletal structures in Rugosa. *J. Fac. Sci. Hokkaido Univ.* (4, geol. min.) **11** : 571–630, 3 pls.

KAYSER, F. H. E. 1889. Ueber das Devon in Devonshire und im Boulonnais. *Neues Jb. Miner. Geol. Paläont.*, Stuttgart, **1** : 179–191.

LANG, W. D. 1923. Trends in British Carboniferous Corals. *Proc. Geol. Ass.*, London, **34** : 120–136, text-figs. 15–17.

LANG, W. D. & SMITH, S. 1935. *Cyathophyllum caespitosum* Goldfuss, and other Devonian corals considered in a revision of that species. *Q. Jl geol. Soc. Lond.*, **91** : 538–590, pls. 35–37.

LANG, W. D., SMITH, S. & THOMAS, H. D. 1940. *Index of Palaeozoic coral genera*. vii + 231 pp. London.

LECOMPTE, M. 1952. *Madréporaires Paléozoiques*. *In* PIVETEAU, J. (Ed.). *Traité de Paléontologie*, **1** : 419–538, text-figs. 1–154 + 1–75. Paris.

LINNAEUS, C. 1758. *Systema Naturae*, **1** : iv + 823 pp. Editio Decima, Reformata. Stockholm.

LLOYD, W. 1933. The geology of the country around Torquay. [2nd. edn.]. *Mem. geol. Surv. Engld. & Wales*, London : 1–169, pls. 1–7.

LONSDALE, W. 1840. *In* SEDGWICK, A. & MURCHISON, R. I. On the Physical Structure of Devonshire, and on the Subdivisions and Geological Relations of its older stratified Deposits, etc. *Trans. geol. Soc. Lond.* (2nd ser.), **5** : 697, pl. 58.

M'COY, F. 1851–55. *In* SEDGWICK, A. *A Synopsis of the Classification of the British Palaeozoic rocks, by the Rev. Adam Sedgwick, . . . with a systematic Description of the British Palaeozoic Fossils in the Geological Museum of the University of Cambridge by Frederick M'Coy*. i–iv, 1–184 (1851); i–[x], 185–406 (1852); Introduction, i–xcviii, 407–661 (1855); pls. iA–iL, iiA–iiD, iiiA–iiiD. London & Cambridge.

MCLAREN, D. J. 1959. A revision of the Devonian coral genus *Synaptophyllum* Simpson. *Bull. geol. Surv. Can.*, Ottawa, **48** : 15–33, pls. 7–10.

MARTIN, W. 1809. *Petrificata derbiensia; or, figures and descriptions of petrifactions collected in Derbyshire.* ix, ii, ii, [1–102], 1–28, pls. 1–52. Wigan.

MAYR, E., LINSLEY, E. G. & USINGER, R. L. 1953. *Methods and principles of systematic zoology.* ix + 328 pp., 45 text-figs. New York.

MIDDLETON, G. V. 1959. Devonian Tetracorals from South Devonshire, England. *J. Paleont.*, Chicago, **33** : 138–160, pl. 27.

—— 1960. Spilitic rocks in South-east Devonshire. *Geol. Mag.*, London, **97** : 192–207, 2 text-figs.

MOENKE, M. 1954. Genus *Hexagonaria* in the Devonian of the Holy Cross Mts. *Acta geol. pol. palaeont.*, Warszawa, **4** : 445–483, 2 pls. [In Polish with English summary].

MOORE, R. C., HILL, D. & WELLS, J. W. 1956. *Glossary of morphological terms applied to corals. In* MOORE, R. C. (Ed.) *Treatise on Invertebrate Paleontology*, **F** : 245–251. Lawrence, Kansas.

OLIVER, W. A., Jr. 1960. Rugose corals from reef limestones in the Lower Devonian of New York. *J. Paleont.*, Chicago, **34** : 59–100, pls. 13–19.

—— 1964. The Devonian colonial coral genus *Billingsastraea* and its earliest known species. *Prof. Pap. U.S. geol. Surv.*, Washington, **483–B** : iv + 1–5, 2 pls.

ORBIGNY, A. D'. 1849. *Note sur des polypiers fossiles.* 12 pp. Paris.

—— 1850. *Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés*, **1** : ix + 394 pp. Paris.

PEDDER, A. E. H. 1964. Two new genera of Devonian tetracorals from Australia. *Proc. Linn. Soc. N.S.W.*, Sydney, **88** : 364–367, pl. 19.

—— 1966. The Devonian tetracoral *Haplothecia* and new Australian phacellophyllids. *Proc. Linn. Soc. N.S.W.*, Sydney, **90** : 181–189, pl. 6.

PENECKE, K. A. 1894. Das Grazer Devon. *Jb. K. K. geol. Reichsanst.*, Wien, **43** (for 1893) : 567–616, pls. 7–12.

PHILLIPS, J. 1841. *Figures and Descriptions of the Palaeozoic Fossils of Cornwall, Devon and West Somerset.* xii + 231 pp., 60 pls. London.

QUENSTEDT, F. A. VON 1851–52. *Handbuch der Petrefaktenkunde.* [iv] + 1–528, pls. 1–52 (1851); 529–792, pls. 53–62 (1852). Tübingen.

—— 1878–81. *Petrefactenkunde Deutschlands,* **6**. *Die Röhren- und Sternkorallen.* 1–144 (1878); 145–624 (1879); 625–912 (1880); 913–1094 (1881); and Atlas. Leipzig.

ROEMER, C. F. 1852–54. *Kohlen-Periode. In* BRONN, H. G. & ROEMER, C. F. 1851–56. *H. G. Bronn's Lethaea Geognostica* (Dritte Auflage), **1**, 2 : 1–788 and Atlas. Stuttgart.

—— 1883. *Lethaea Geognostica,* **1** Theil. *Lethaea palaeozoica,* 1, 2 : 325–544, text-figs. 62–126 + Atlas. Stuttgart.

ROEMER, F. A. 1843. *Die Versteinerungen des Harzgebirges.* [8] + xx + 1–40, pls. 1–12. Hannover.

—— 1855. Beitrage zur geologischen Kenntniss des nordwestlichen Harzgebirges. Dritte Abtheilung. *Palaeontographica,* **5** : [iv] + 1–44, pls. 1–8.

RÓŻKOWSKA, M. 1953. Pachyphyllinae et *Phillipsastraea* du Frasnien de Pologne. *Palaeont. pol.*, Warszawa, **5** : 1–89, 8 pls.

—— 1956. Pachyphyllinae from the Middle Devonian of the Holy Cross Mts., Part 1. *Acta palaeont. pol.*, Warszawa, **1** : 271–330, 39 text-figs.

—— 1957. Considerations on Middle and Upper Devonian Thamnophyllidae Soshkina in Poland, Part 2. *Acta palaeont. pol.*, Warszawa, **2** : 81–153, 27 text-figs.

—— 1960. Blastogeny and individual variations in tetracoral colonies from the Devonian of Poland. *Acta palaeont. pol.*, Warszawa, **5** : 3–64, 43 text-figs.

—— 1965. Marisastridae n. fam. and *Marisastrum* n. gen. (Devonian corals). *Acta palaeont. pol.*, Warszawa, **10** : 261–266, 2 text-figs.

SANDBERGER, G. & SANDBERGER, F. 1856. *Die Versteinerungen des rheinischen Schichtensystems in Nassau,* **8–9** : 233–564 + i–xv, Atlas pls. 34–41. Wiesbaden.

SANFORD, W. G. 1939. A review of the Families of Tetracorals. *Am. J. Sci.*, New Haven, **237** : 295–323, text-figs. 1–10; 401–423, text-figs. 11–16.

SCHAFER, R. 1889. On *Phillipsastraea* d'Orb., with special reference to *Phillipsastraea radiata* S. Woodward sp. and *Phillipsastraea tuberosa* M'Coy sp. *Geol. Mag.*, London, **6** : 398–409, pl. 12.

SCHLÜTER, C. 1881. Ueber einige Anthozoen des Devon. *Z. dt. geol. Ges.*, Berlin, **33** : 75–108, pls. 6–13.

SCHOUPPÉ, A. VON 1949. Die " Thamnophyllen " und ihre Beziehungen zur Gruppe des " *Cyathophyllum caespitosum* ". *Palaeontographica*, Stuttgart (A) **47** : 99–180, pls. 9–14.

—— 1956. Neue Betrachtungen zur Skelettbildung der Pterocorallia. *Paläont. Z.*, Berlin, **30** : 148–162, 5 text-figs.

—— 1958. Revision des Formenkreises um *Phillipsastraea* d'Orb., " *Pachyphyllum* " E. & H., *Macgeea* (Webst.), " *Thamnophyllum* " Pen., *Peneckiella* Soshk. und verwandter Formen. *Neues Jb. Geol. Paläont. Abh.*, Stuttgart, **106** : 139–244, pls. 5, 6.

SCHOUPPÉ, A. VON & STACUL, P. 1963. Bau und taxionomische Fassung des devonischen Korallen-Genus *Macgeea* Webster 1889 und seine Beziehungen zu *Thamnophyllum* Penecke 1894. *Senckenburg. leth.*, Frankfurt a.M., **44** : 265–299, pl. 41.

SCHWEIGGER, A. F. 1819. *Beobachtungen auf Naturhistorischen Reisen.* xii + 127 pp., 8 pls. Berlin.

SCRUTTON, C. T. 1965. The ages of some coral faunas in the Torquay area. *Proc. Ussher Soc.*, Redruth, **1** : 186–188, 3 text-figs.

—— 1967. Marisastridae (Rugosa) from south-east Devonshire, England. *Palaeontology*, London, **10** : 266–279, pls. 40–43.

SEMENOFF-TIAN-CHANSKY, P. 1961. Madréporaires paléozoïques. *In* SEMENOFF-TIAN-CHANSKY, P., LAFUSTE, J. & DELGA, M. D. Madréporaires du Dévonien du Chénoua (Algérie). *Bull. Soc. géol. Fr.*, Paris (7) **3** : 292–313, pl. 9.

SIMPSON, G. G., ROE, A. & LEWONTIN, R. C. 1960. *Quantitative zoology.* vii + 440 pp., 64 text-figs. New York.

SMITH, S. 1917. *Aulina Rotiformis*, gen. et sp. nov. *Phillipsastraea Hennahi* (Lonsdale), and *Orionastraea*, gen. nov. *Q. Jl geol. Soc. Lond.*, **72** : 280–307, pls. 22–24.

—— 1945. Upper Devonian corals of the Mackenzie River region, Canada. *Spec. Pap. geol. Soc. Am.*, New York, **59** : viii + 1–126, pls. 1–35.

SOSHKINA, E. D. 1939. Verkhnedevonskie korally Rugosa Urala. *Trudy paleont. Inst.*, Leningrad, **9** : 1–88, pls. 1–14. [In Russian with English summary].

—— 1949. Devonskie korally Rugosa Urala. *Trudy paleont. Inst.*, Leningrad, **15** : 1–160, pls. 1–58 [In Russian].

—— 1951. Pozdnedevonskie korally Rugosa, ikh sistematika i evolyutsiya. *Trudy paleont. Inst.*, Leningrad, **34** : 1–122, pls. 1–24. [In Russian].

—— 1952. Opredelitel devonskikh chetyrekhluchevykh korallov. *Trudy paleont. Inst.*, Leningrad, **39** : 1–127, pls. 1–49. [In Russian].

—— 1953. Tsenogeneticheskie prisposobleniya u nekotorykh devonskikh korallov Rugosa. *Ezheg. vses. paleont. Obshch.*, Moscow, **14** : 80–90, text-figs. 1–14. [In Russian].

—— 1954. Devonski chetyrekhluchevye korally Russkoi Platformy. *Trudy paleont. Inst.*, Leningrad, **52** : 1–76, pls. 1–19. [In Russian].

—— 1962. *Podotryad* Cystiphyllina. *In* ORLOV, U. A. (Ed.) *Osnovy paleontologii*, **2**. *Gubki, Arkheotsiaty, Kishechnopolostnye, Chervi* : 306–311, pls. 1, 2 and pl. 3, figs. 1, 2. Moscow. [In Russian].

SOSHKINA, E. D. & DOBROLUBOVA, T. A. 1962. *Otryad* Evenkiellida. *In* ORLOV, U. A. (Ed.) *Osnovy palaeontologii*, **2**. *Gubki, Arkheotsiaty, Kishechnopolostnye, Chervi* : 333–339, pls. 17–21. Moscow. [In Russian].

SPASSKY, N. YA. 1960. *Paleontologicheskoe obosnovanie stratigrafii paleozoya Rudnogo Altaya; vypusk* **3**. *Devonskie chetyrekhluchevye Korally Rudnogo Altaya.* 143 pp., 35 pls. Moscow. [In Russian].

STEPHENSON, T. A. 1931. Development and the formation of colonies in *Pocillopora* and *Porites*. *Brit. Mus. (Nat. Hist.) Great Barrier Reef Exped. Sci. Rept.*, London, **3**, 3 : 113–134, pls. 1–6.

STRUSZ, D. L. 1965. Disphyllidae and Phacellophyllidae from the Devonian Garra Formation of New South Wales. *Palaeontology*, London, **8** : 518–571, pls. 72–78.

STUMM, E. C. 1949. Revision of the families and genera of the Devonian tetracorals. *Mem. geol. Soc. Am.*, New York, **40** : viii + 1–92, pls. 1–25.

TAYLOR, P. W. 1951. The Plymouth Limestone. *Trans. R. geol. Soc. Corn.*, Penzance, **18** : 146–214, pls. 1–5.

TORLEY, K. 1934. Die Brachiopoden des Massenkalks der oberen Givet-Stufe von Bilveringsen bei Iserlohn. *Abh. Senckenb. naturforsch. Ges.*, Frankfurt a.M., **43**, 3: 67–148, pls. 1–9.

USSHER, W. A. E. 1903. The geology of the country around Torquay. *Mem. geol. Surv. Engld. & Wales*, London : i–iv + 1–142, 17 text-figs.

USSHER, W. A. E. *et al.* 1913. The geology of the country around Newton Abbot. *Mem. geol. Surv. Engld. & Wales*, London : i–vi + 1–149, 3 pls.

VERNEUIL, E. DE & HAIME, J. 1850. *In* VERNEUIL, E. DE. Note sur les fossiles dévoniens du district de Sabero (Léon). *Bull. Soc. géol. Fr.*, Paris (2) **7** : 161–162.

VOYNOVSKIY-KRIGER, K. G. 1954. O dinamike razvitiya septalnogo apparata v ontogeneze chetyrekhluchevykh. *Byull. mosk. Obshch. Ispyt. Prir.*, Moscow, **59**, otdel, geol., 29, 5 : 51–64, text-figs. 1–11. [In Russian].

WALTHER, C. 1929. Untersuchungen über die Mitteldevon- Oberdevongrenze. *Z. dt. geol. Ges.*, Berlin, **80** (for 1928) : 97–152, text-figs. 1–34.

WANG, H. C. 1950. A revision of the Zoantharia Rugosa in the light of their minute skeletal structures. *Phil. Trans. R. Soc.*, London (B) **234** : 175–246, pls. 4–9.

WEBBY, B. D. 1964. Devonian corals and brachiopods from the Brendon Hills, west Somerset. *Palaeontology*, London, **7** : 1–22, pl. 1.

WEBSTER, C. L. 1889. Description of a New Genus of Corals, from the Devonian Rocks of Iowa. *Am. Nat.*, Lancaster, Pa., **23**, 272 : 710–712.

WEDEKIND, R. 1922. Zur Kenntnis der Stringophyllen des oberen Mitteldevon. *Sber. Ges. Beförd. ges. Naturw. Marburg*, 1921, 1 : 1–16, text-figs. 1–18.

WHIDBORNE, G. F. 1888–1907. A monograph of the Devonian fauna of the south of England, Part 1 : 1–344, pls. 1–31; Part 2 : 1–222, pls 1–24; Part 3 : 1–247, pls. 1–38. *Palaeontogr. Soc.* [*Monogr.*], London.

ADDENDUM

Whilst this paper was in press, J. E. Sorauf, (1967, *Paleont. Contr. Univ. Kans.*, **16** : 1–41) published a work describing phillipsastraeids from the Frasnian of Belgium. The opportunity is taken here to comment briefly on some of the more important points discussed by Sorauf which bear closely on the present paper.

Sorauf (pp. 5, 15) introduces the term " pseudocerioid ", which he defines and uses in precisely the same way as in the present paper. It is gratifying to note that independent work by Sorauf and the writer on the same species (principally *Frechastraea goldfussi* and *F. pentagona*) has led to the same interpretation of the corallite wall structure. Sorauf (p. 5), however, infers that species of *Phillipsastrea* and the Phillipsastraeidae are never cerioid whereas the genus and family as defined here do include massive forms with an epitheca between at least some of the corallites (this paper, p. 210).

Sorauf (p. 13) separates *Phillipsastrea* and *Pachyphyllum* by restricting the latter genus to species with a perfect single series of horseshoe dissepiments. In *Phillipsastrea* he includes a complete range of dissepimental form, from specimens lacking any sign of horseshoe dissepiments to those in which an almost complete series is present. In fact this whole range is represented in Sorauf's concept of a single species of *Phillipsastrea, P. hennahi* (fig. 5, 1c and 2).

Apart from the difference in the degree of development of the horseshoe dissepiments, species of *Phillipsastrea* and *Pachyphyllum* show no significant divergence in their basic morphology to warrant generic separation. Moreover, when the development of horseshoe dissepiments is closely examined even this criterion is, in the writer's opinion, impossible to maintain (compare the longitudinal-section of a topotype of *Pachyphyllum bouchardi* (Semenoff-Tian-Chansky 1961, pl. 9, fig. 2) with a section attributed by Sorauf (fig. 5, 2) to *Phillipsastrea hennahi*).

The writer is also unable to agree with Sorauf's (p. 26) interpretation of *Phillipsastrea hennahi*. None of the illustrations (figs. 5, 1*a–c*; 8, 1*a–d*: figs. 5, 1*d–e*; 5, 2 are longitudinal-sections only) is considered consubspecific with *Phillipsastrea hennahi hennahi* herein, whilst two specimens (figs. 5, 2; 8, 1*a–b*) are possibly consubspecific with *P. hennahi ussheri* subsp. nov. The significance of this should not be overlooked. *P. hennahi hennahi* appears to be characteristic of the middle and upper Givetian of England (this paper, p. 216), not of the Frasnian as stated by Sorauf (pp. 23, 27). On the other hand, the subspecies *P. hennahi ussheri* is found in the English Lower Frasnian.

The same English Lower Frasnian limestones yield *Frechastraea pentagona pentagona* and *F. pentagona minima*. Both subspecies were considered, the latter by inference, to be upper Frasnian index forms by Sorauf (pp. 31, 33).

PLATE 1

Phillipsastrea hennahi hennahi (Lonsdale)

FIG. 1. Cross-section (slide). GSM PF1245 (cut from lectotype). ×3.

FIGS. 2, 3. Longitudinal-sections (slide). GSM PF1249 (cut from lectotype). ×4.

FIG. 4. Longitudinal-section (peel). GSM PF4028 (taken from lectotype). ×4.

Figs. 1–4 all upper Givetian, Barton Quarry.

FIG. 5. Longitudinal-section (peel). TM(JB) 79; upper Givetian, Lummaton Quarry. ×4.

FIG. 6. Longitudinal-section (peel). GSM PF4028 (taken from lectotype); upper Givetian, Barton Quarry. ×4.

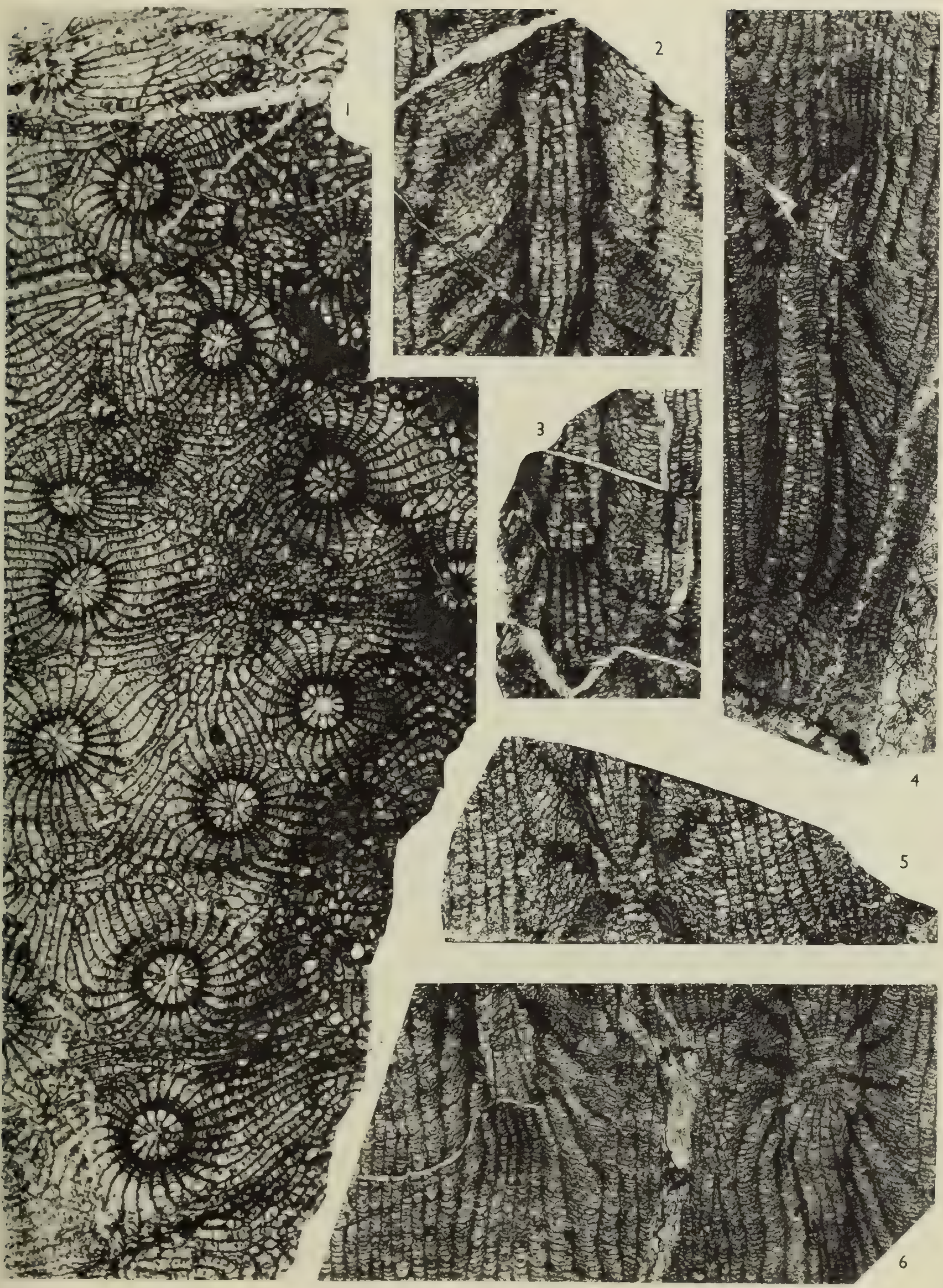

1
2
3
4
5
6

PLATE 2

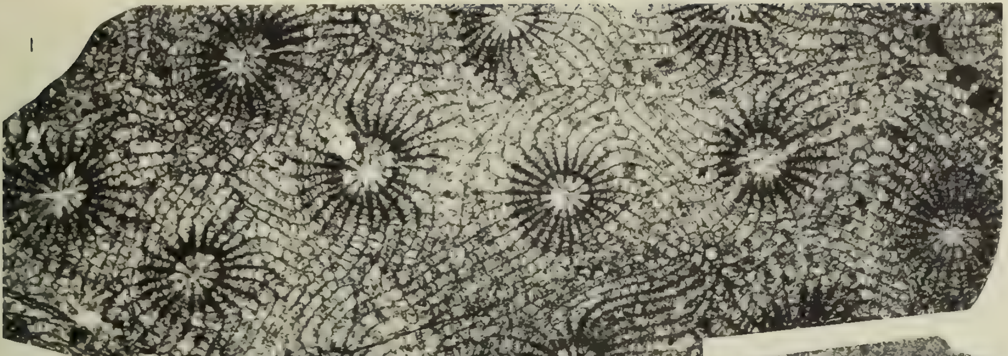
Phillipsastrea hennahi hennahi (Lonsdale)

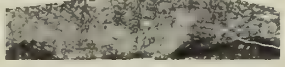
Fig. 1. Cross-section (peel). TM(JB) 79; upper Givetian, Lummaton Quarry. ×3.

Fig. 2, 3. Cross- and longitudinal-sections (peels). OUM D74/p1 (from holotype of *Astraea intercellulosa* Phillips); ?Middle Devonian, Torquay. ×2.

Fig. 4. Cross-section (peel). GSM PF4029 (from lectotype of *Syringophyllum cantabricum* Edwards & Haime); ?Middle Devonian, Torquay. ×2.

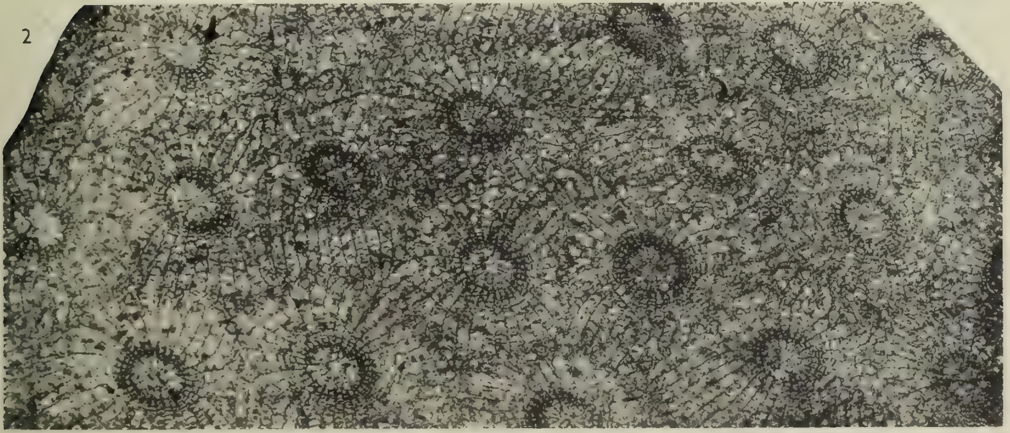
1

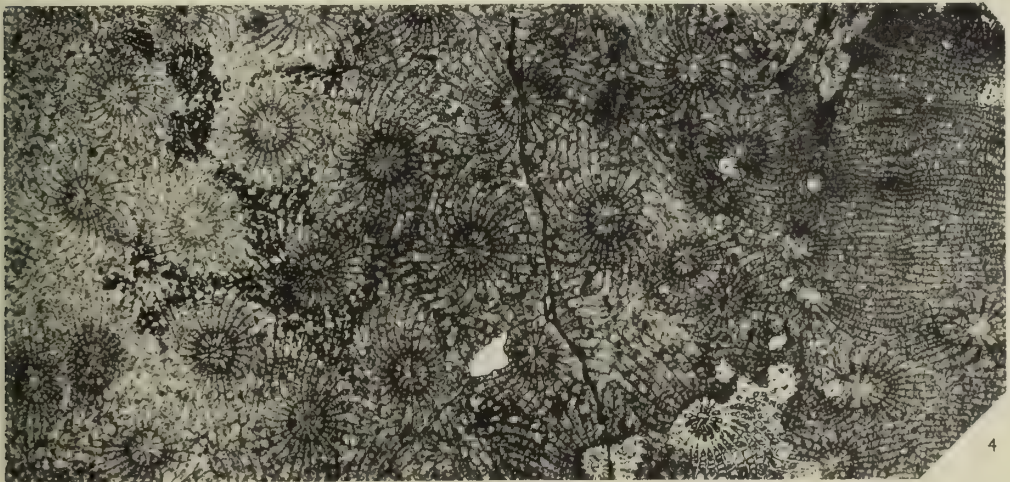




3

2





4

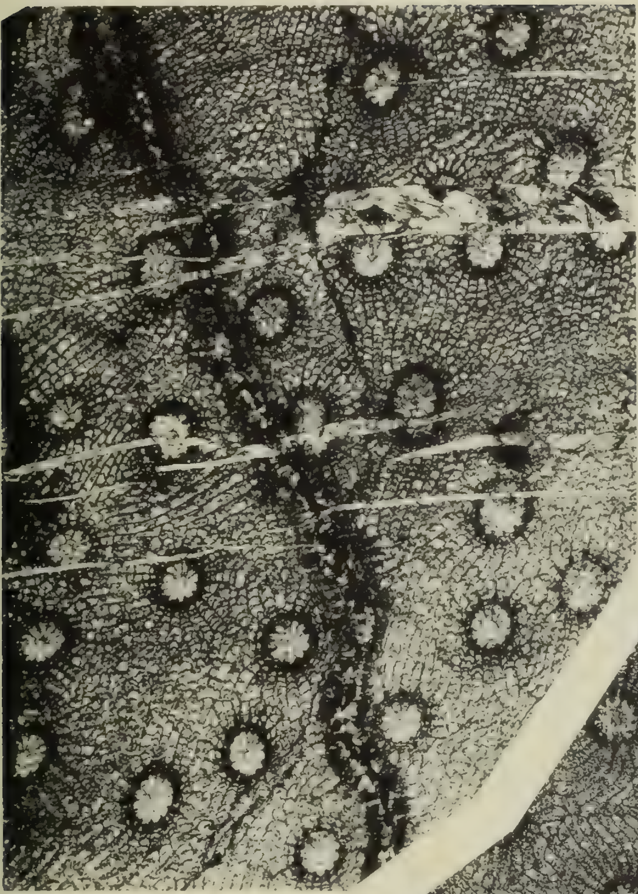
PLATE 3

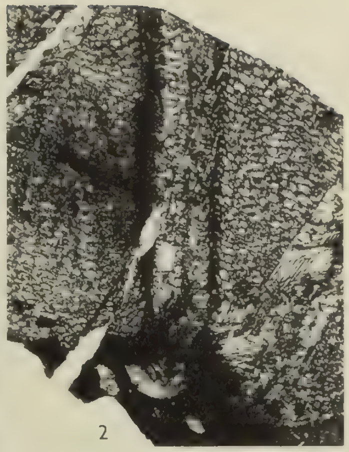
Phillipsastrea hennahi ussheri subsp. nov.

FIG. 1. Cross-section (slide). OUM D544/p 1. ×3.
FIG. 2. Longitudinal-section (slide). OUM D544/p2. ×5.

Both cut from holotype; Lower Frasnian, road cutting 20 yd. west of Ramsleigh Quarry entrance.

FIG. 3. Cross-section (peel). BM(NH) R5616; Lower Frasnian, Ramsleigh Quarry. ×3.


1


2

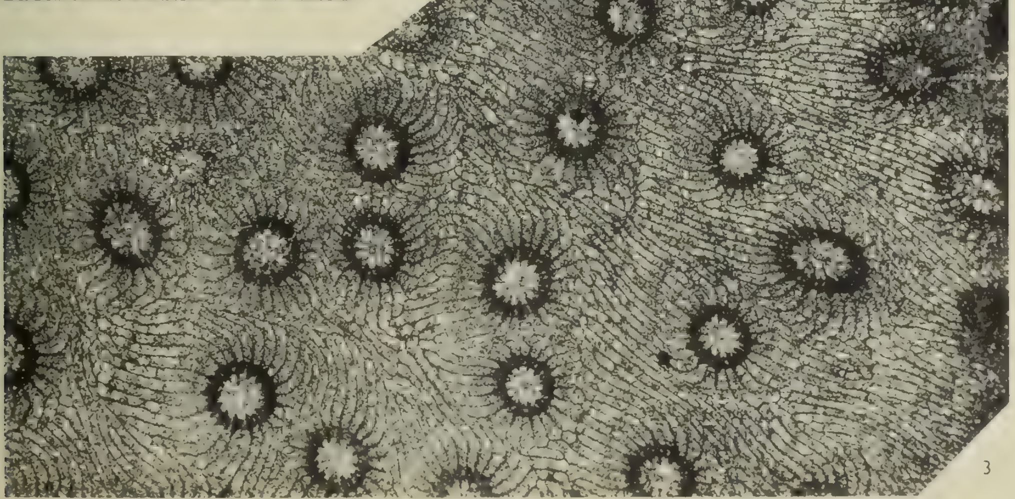

3

PLATE 4

Phillipsastrea devoniensis (Edwards & Haime)

FIG. 1. Cross-section (peel). OUM D277/p1; ?Middle Devonian, Rocky Valley, Torquay. ×2.

FIG. 2. Cross-section (slide). BM(NH) R29996; Middle Devonian, Torquay. ×2.

FIG. 3. Longitudinal-section (peel). ×3.

FIG. 4. Cross-section (peel). ×2.

Figs. 3 and 4 both TM(JB) 105; (?) upper Givetian, Lummaton Quarry.

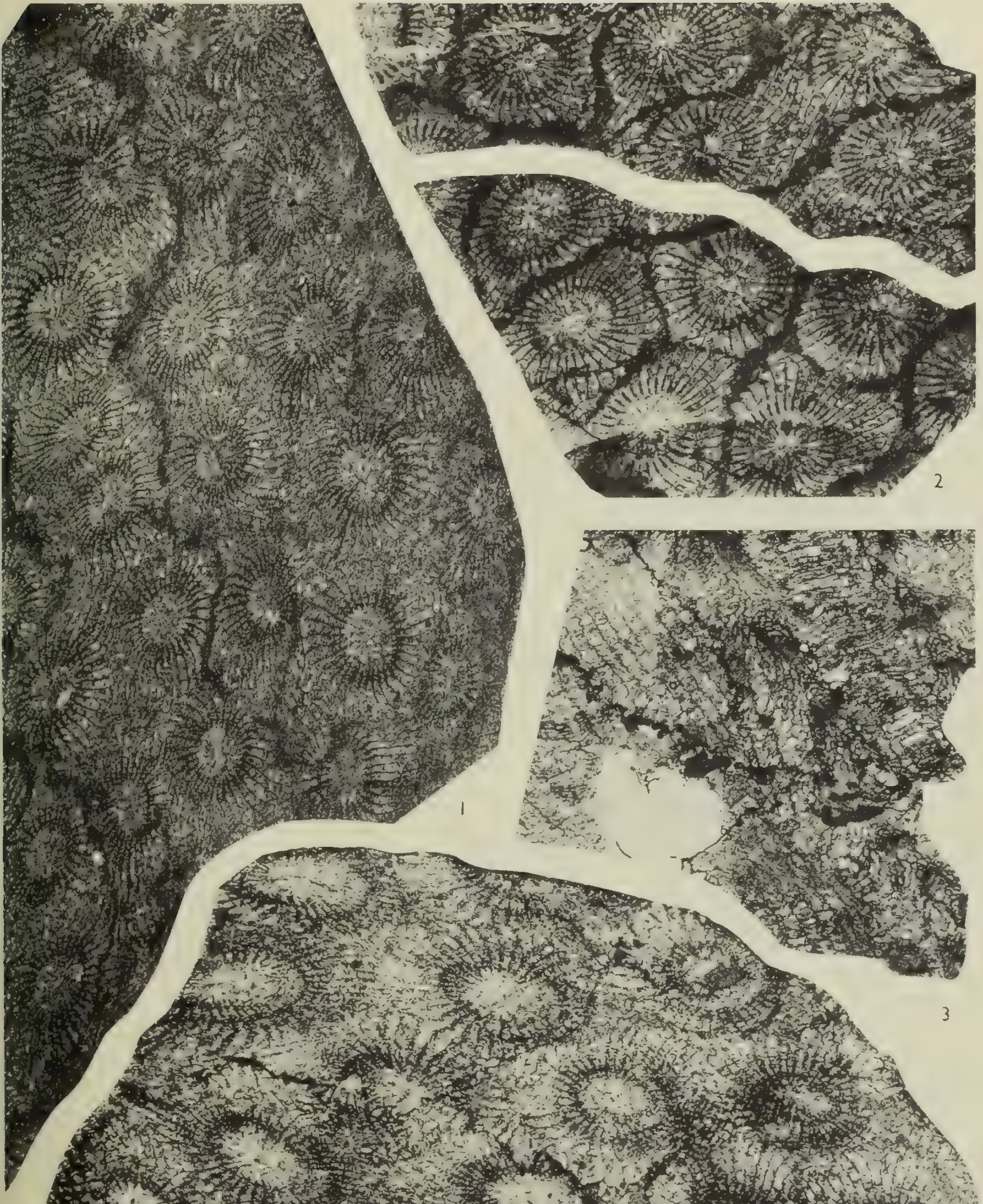
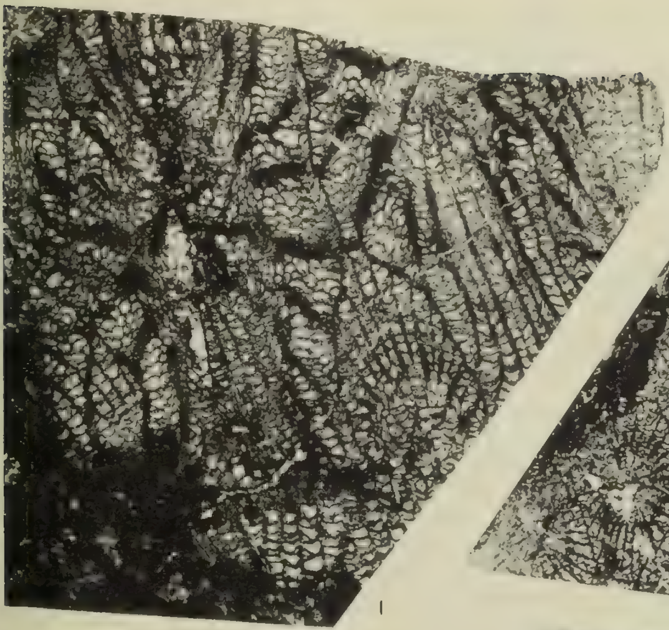

1
2
3
4

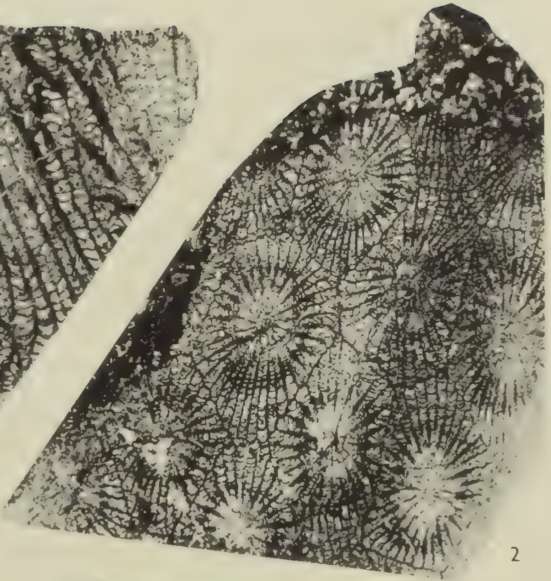
PLATE 5

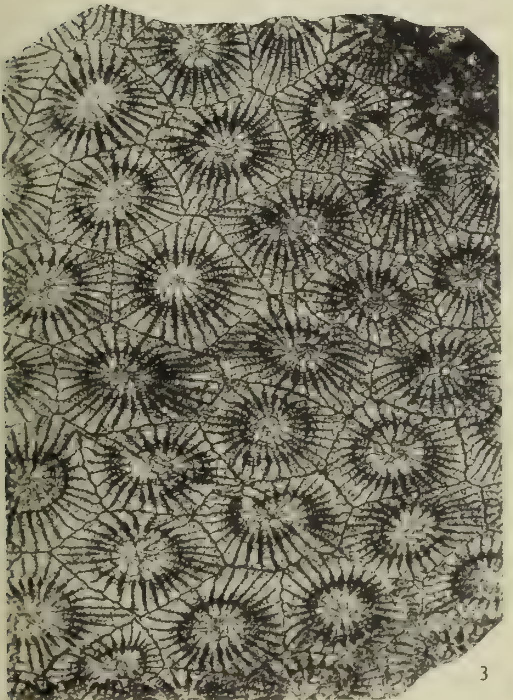
Phillipsastrea ananas (Goldfuss)

FIG. 1. Longitudinal-section (slide). BM(NH) R46158*c*. ×4.
FIG. 2. Cross-section (slide). BM(NH) R46158*a*. ×2.
FIG. 3. Cross-section (slide). BM(NH) R46159*a*. ×2.
FIG. 4. Longitudinal-section (slide). BM(NH) R46159*b*. ×4.

All Lower Frasnian, road cutting south side 30–35 yds. west of Ramsleigh Quarry entrance.


1


2


3

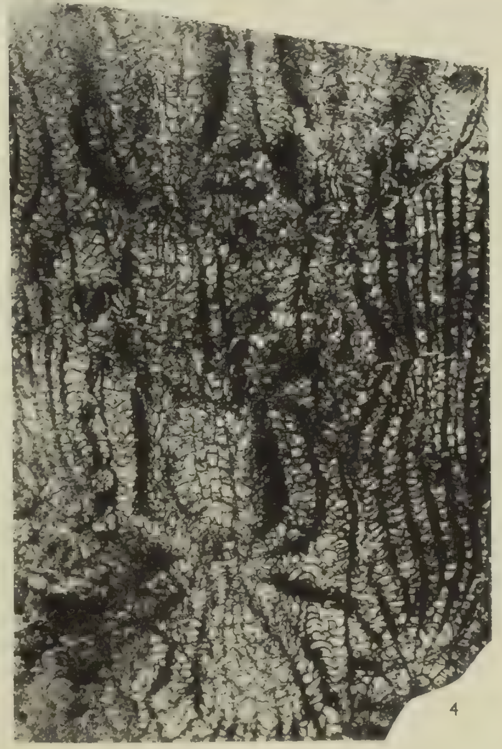

4

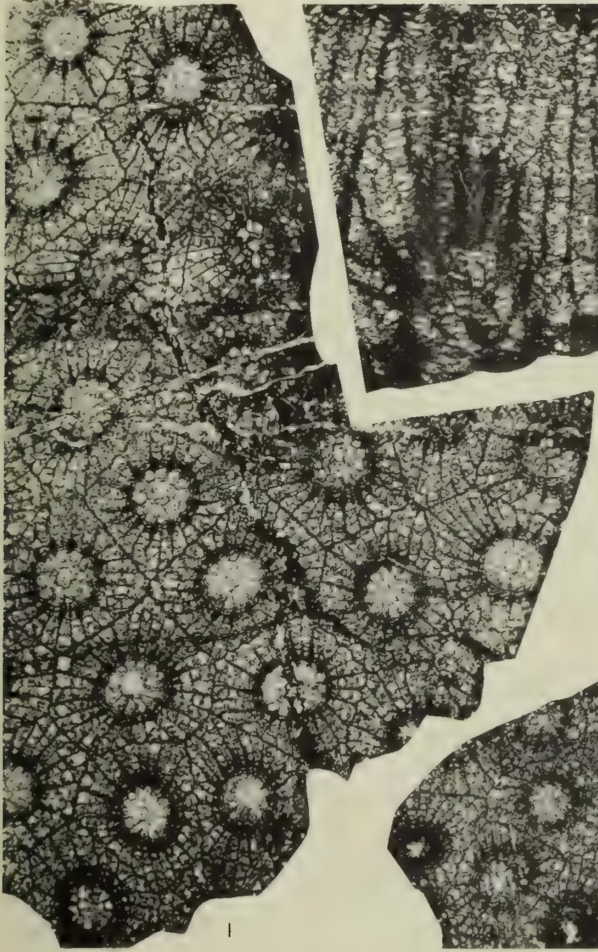
PLATE 6

Phillipsastrea rozkowskae sp. nov.

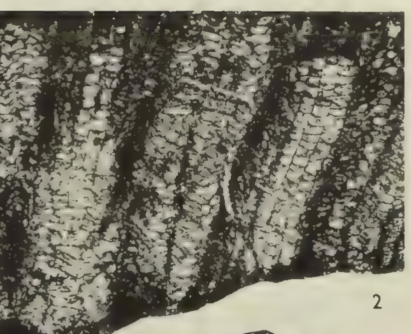
FIG. 1. Cross-section (slide). BM(NH) R46156*a* (cut from holotype). ×2·5.
FIGS. 2, 3. Longitudinal-sections (slide). BM(NH) R46156*b* (cut from holotype). ×5.
FIG. 4. Cross-sections (slide). BM(NH) R46157*a*. ×2·5.
All Lower Frasnian, road cutting south side 25 yds. west of Ramsleigh Quarry entrance.

Frechastraea pentagona pentagona (Goldfuss)

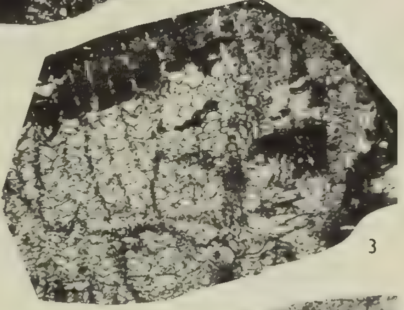
FIG. 5. Cross-section (slide). OUM D537/p1; Lower Frasnian, road cutting 20 yds. west of Ramsleigh Quarry entrance. ×4.



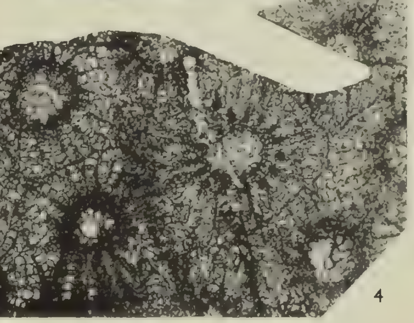
1



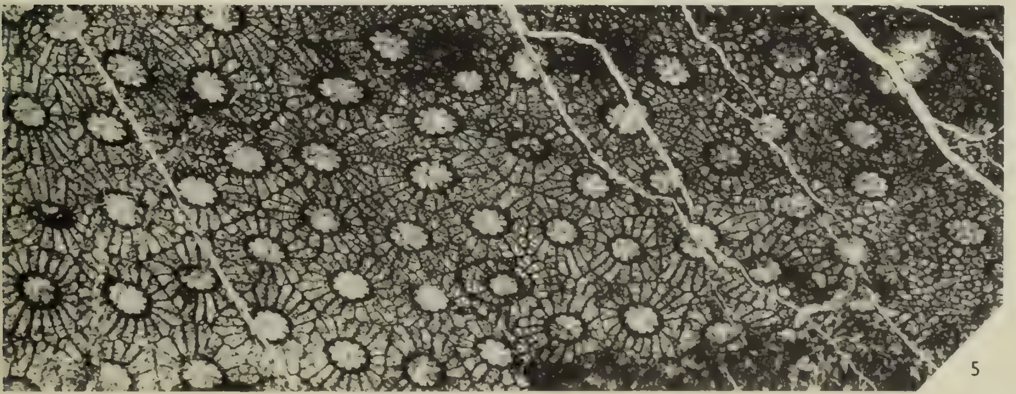
2



3



4



5

PLATE 7

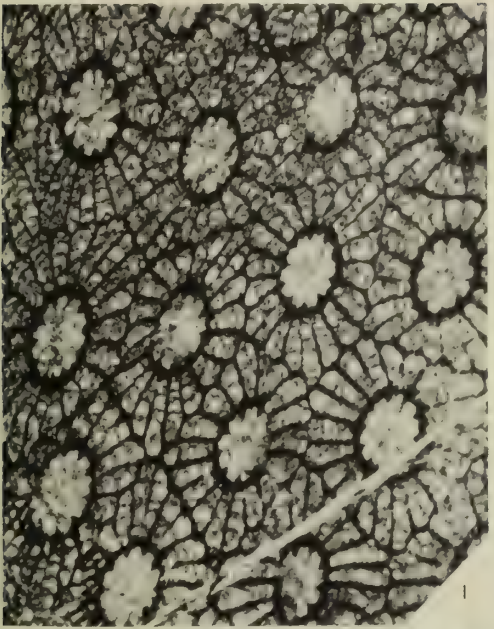
Frechastraea pentagona pentagona (Goldfuss)

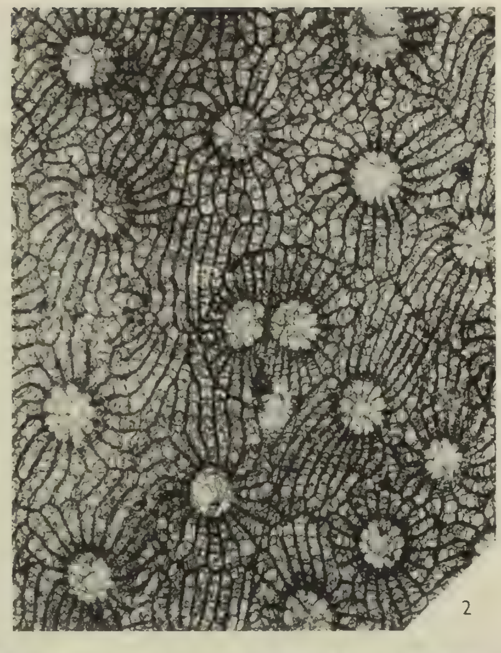
FIG. 1. Cross-section (slide). OUM D537/p1; Lower Frasnian, road cutting 20 yds. west of Ramsleigh Quarry entrance. ×8.

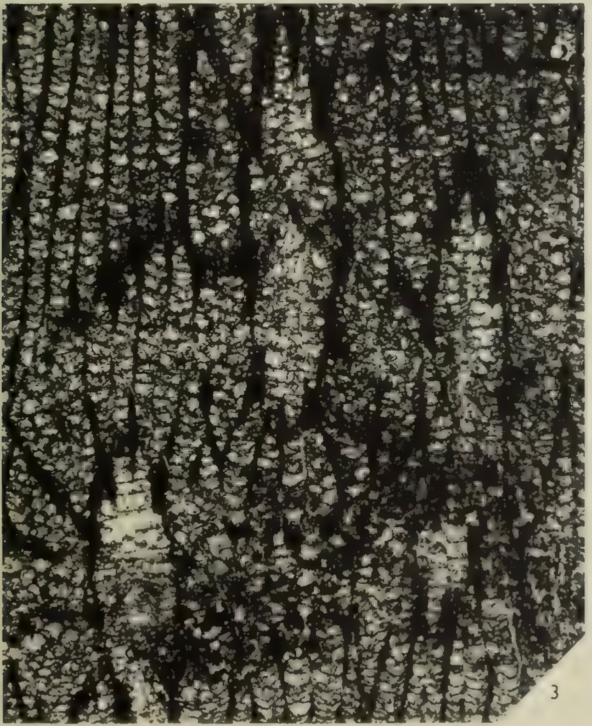
FIG. 2. Cross-section (peel). OUM D279/p1; Lower Frasnian, Ramsleigh Quarry. ×6.

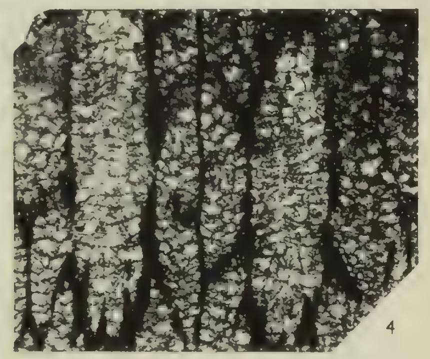
FIGS. 3, 4. Longitudinal-sections (slide). OUM D537/p2; Lower Frasnian, road cutting 20 yds. west of Ramsleigh Quarry entrance. ×8.

FIG. 5. Longitudinal-section (slide). Geol.-Pal. Inst. Bonn, Goldfuss Colln. 206 (cut from lectotype); Frasnian, Namur, Belgium. ×8.


1


2


3


4

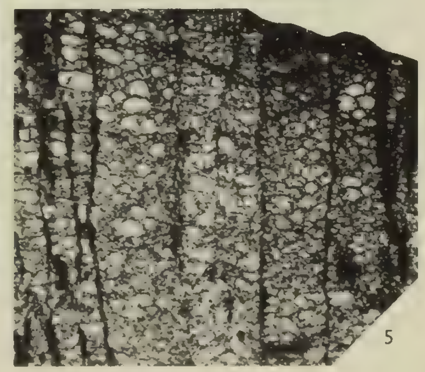

5

PLATE 8

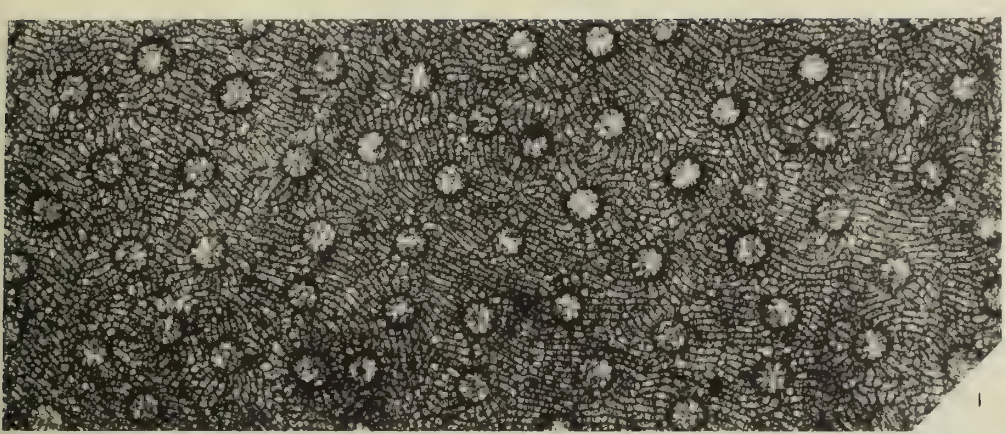
Frechastraea pentagona (Goldfuss) ***minima*** (Różkowska)

FIG. 1. Cross-section (peel). GSM PF4031 (taken from GSM 73118); Lower Frasnian, Ramsleigh Quarry. ×4.

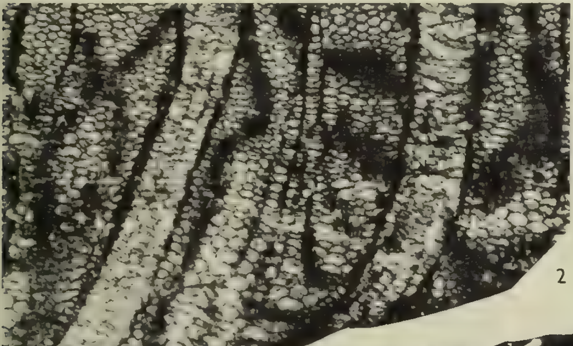
FIGS. 2, 3. Longitudinal-sections (slide). GSM PF4032 (cut from GSM 73118); Lower Frasnian, Ramsleigh Quarry. ×8.

Frechastraea micrommata (C. F. Roemer)

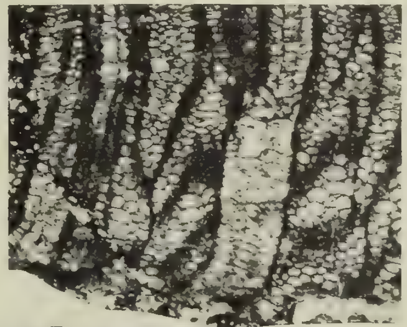
FIGS. 4, 5. Cross- and longitudinal-sections (slides). Geol.-Pal. Inst. Bonn 34 (cut from lectotype); Frasnian, Ferques near Boulogne, France. ×4.



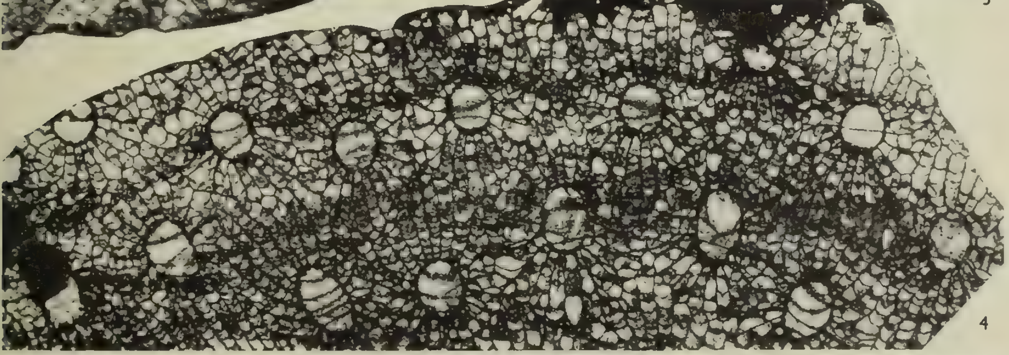
1



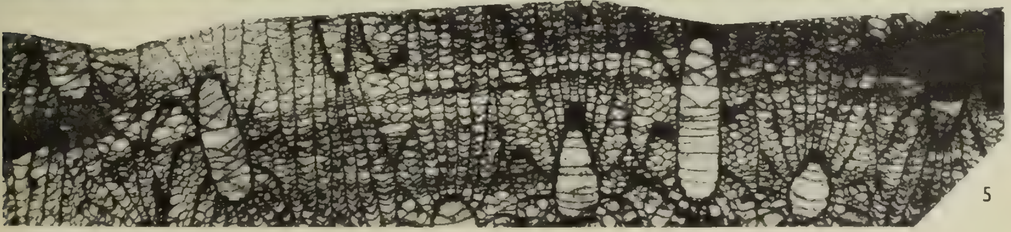
2



3



4



5

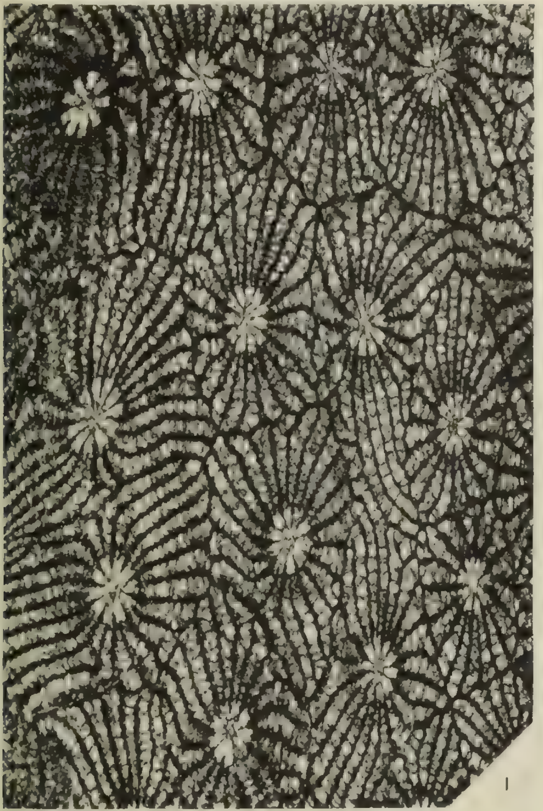
PLATE 9

Frechastraea carinata sp. nov.

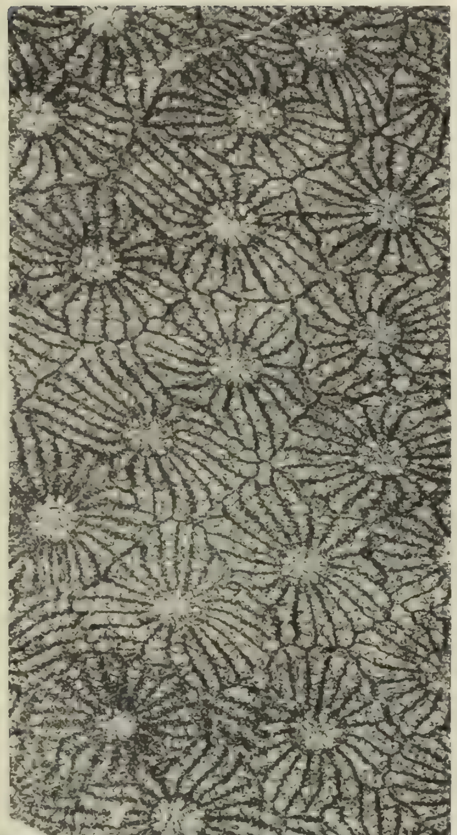
FIG. 1. Cross-section (slide). OUM D309*b* (cut from holotype); Lower Frasnian, road cutting 80 yds. west of Ramsleigh Quarry entrance. ×6.

FIG. 2. Cross-section (peel). BM(NH) R5634; Lower Frasnian, Ramsleigh Quarry. ×6.

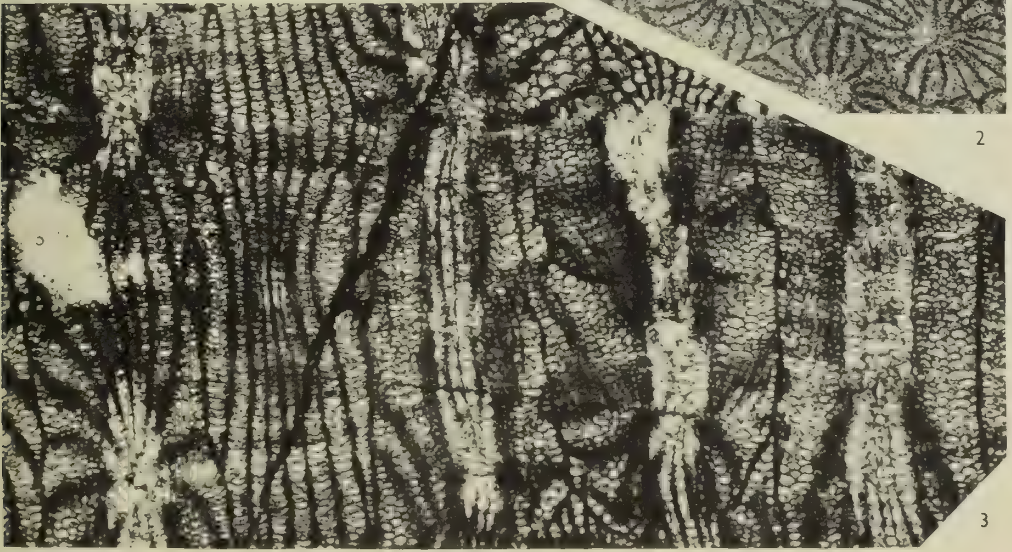
FIG. 3. Longitudinal-section (slide). OUM D309*d* (cut from holotype); Lower Frasnian, road cutting 80 yds. west of Ramsleigh Quarry entrance. ×6.



1



2

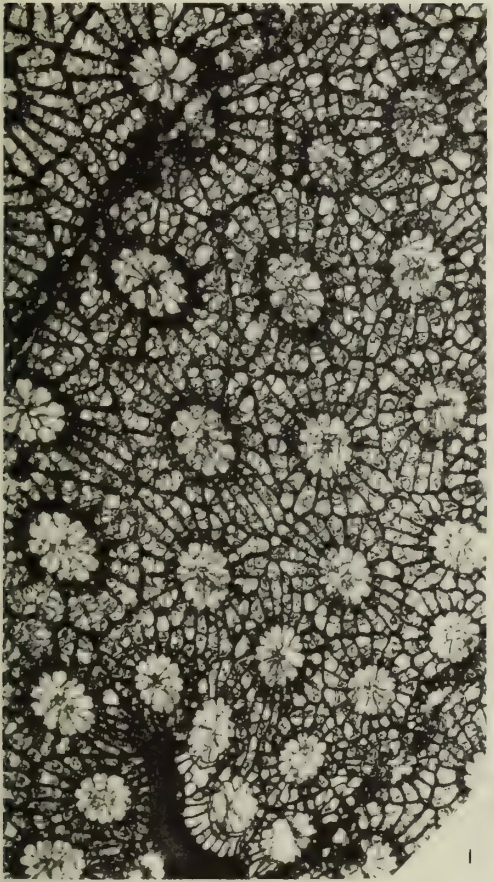


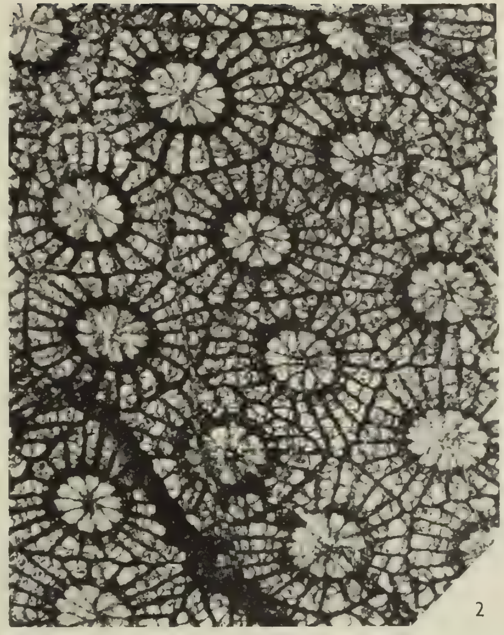
3

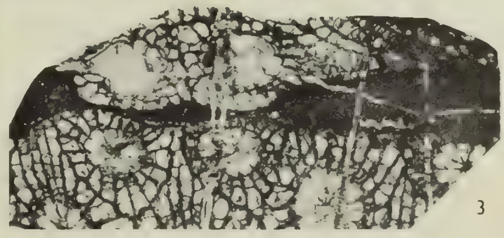
PLATE 10

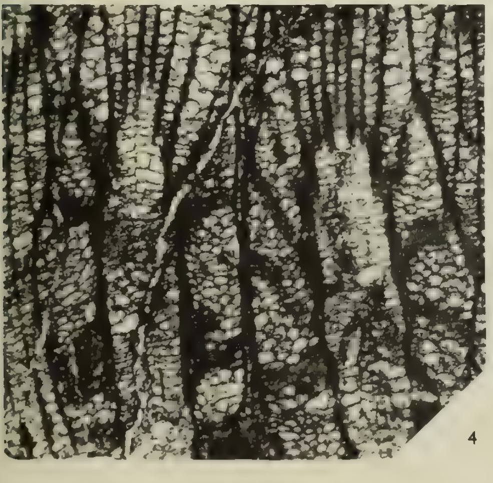
Frechastraea goldfussi (de Verneuil & Haime)

Fig. 1. Cross-section (slide). OUM D540/p2. ×5.
Figs. 2, 3. Cross-sections (slide). OUM D539/p2. ×5.
Fig. 4. Longitudinal-section (slide). OUM D541/p2. ×6.
Fig. 5. Longitudinal-section (slide). OUM D540/p1. ×8.
All Lower Frasnian, Ramsleigh Quarry.


1


2


3


4

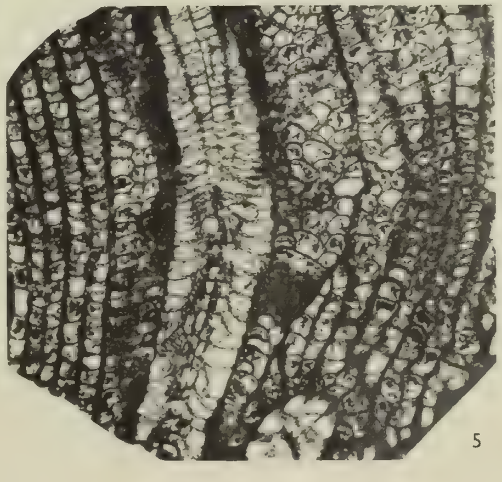

5

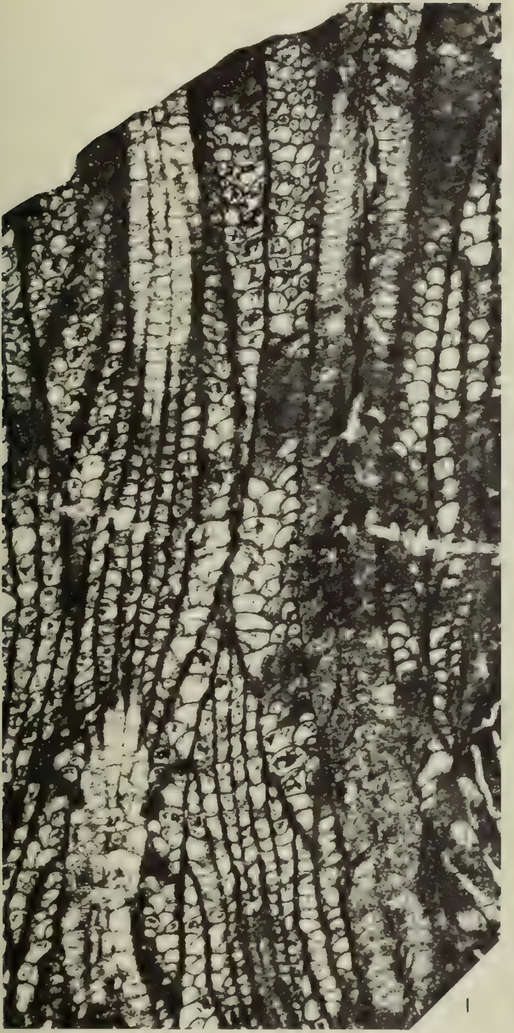
PLATE 11

Frechastraea goldfussi (de Verneuil & Haime)

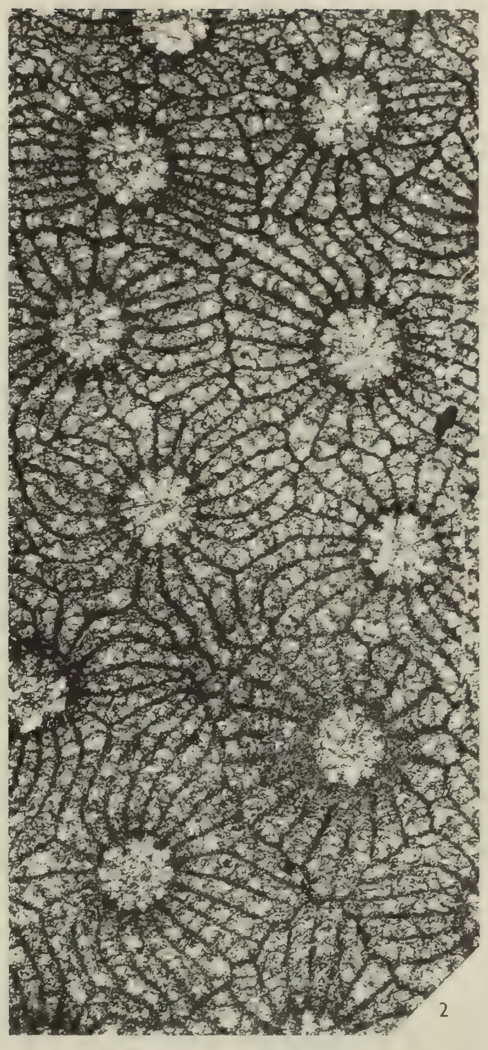
Fig. 1. Longitudinal-section (slide). OUM D540/p1. ×8.
Fig. 2. Cross-section (peel). TM(JB) 318. ×7.
Figs. 1 and 2 both Lower Frasnian, Ramsleigh Quarry.

Frechastraea bowerbanki (Edwards & Haime)

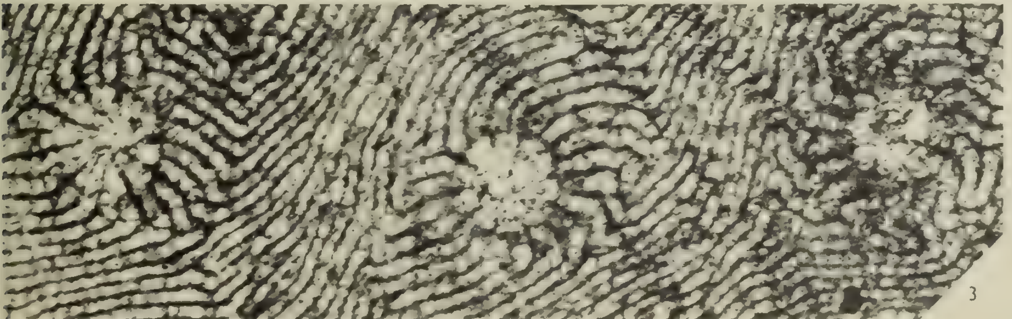
Fig. 3. Cross-section (peel). TM 136/7; Lower Frasnian, Ramsleigh Quarry. ×10.



1



2



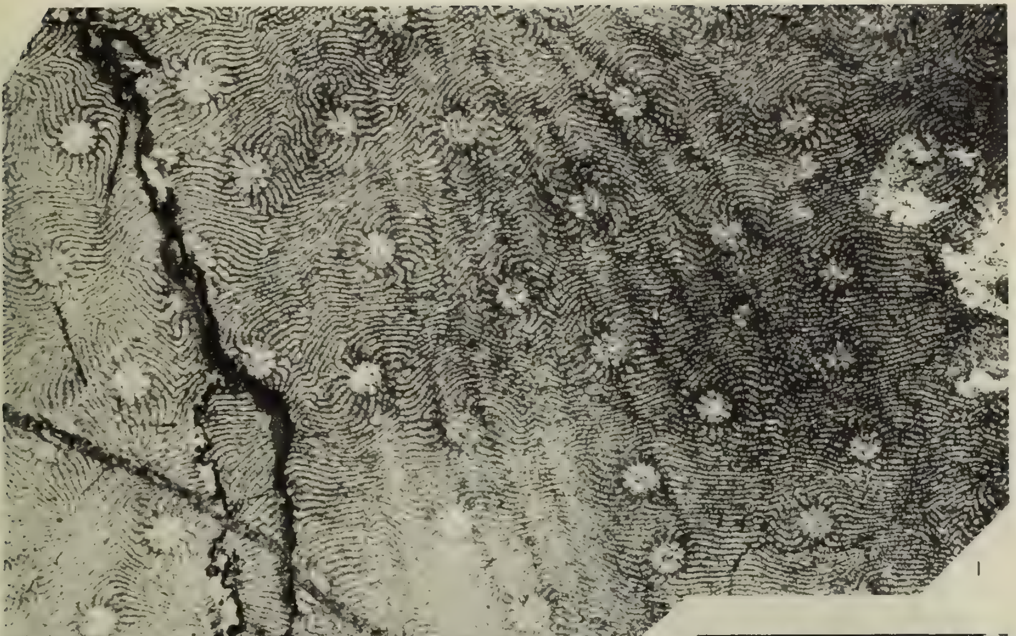
3

PLATE 12

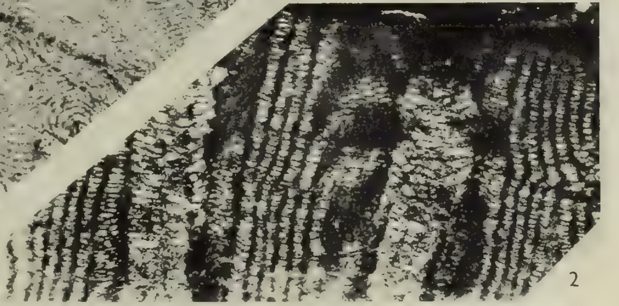
Frechastraea bowerbanki (Edwards & Haime)

FIG. 1. Cross-section (peel). TM 136/7. ×3.
FIG. 2. Longitudinal-section (slide). BM(NH) R46373. ×6.
FIG. 3. Longitudinal-section (slide). TM 136/7. ×6.

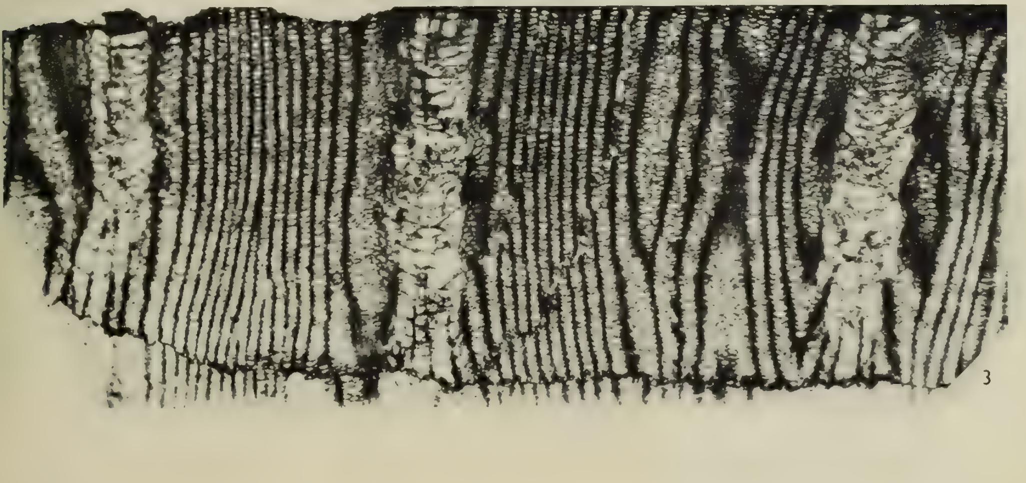
All Lower Frasnian, Ramsleigh Quarry.



1



2



3

PLATE 13

Thamnophyllum germanicum schouppei nom. nov.

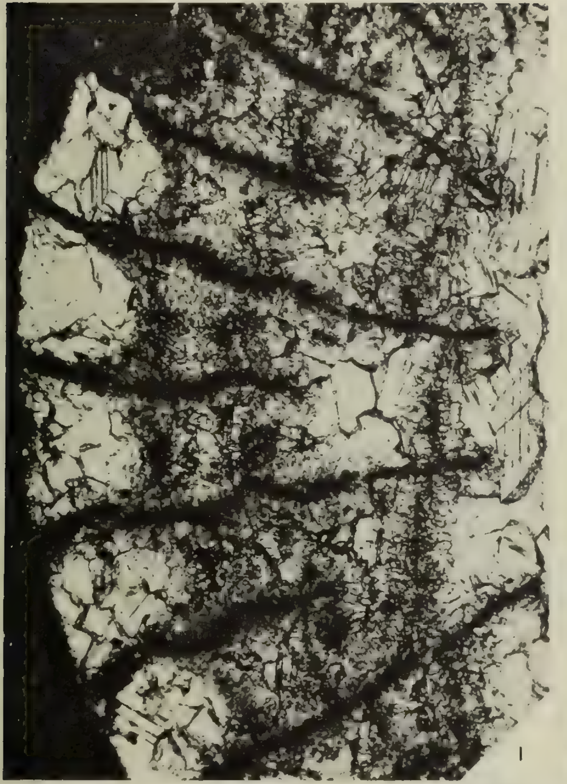
FIG. 1. Cross-section (slide). OUM D509/p1; lower Givetian, Dyer's Quarry. ×50.

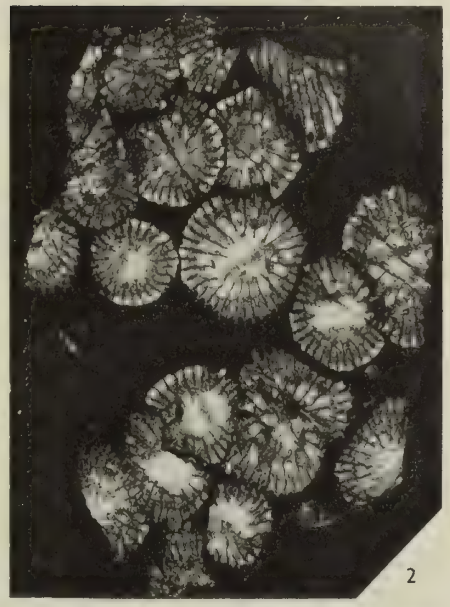
FIG. 2. Cross-section (slide). Pal. Inst. Graz UPG 327 (cut from holotype); Middle Devonian, Torquay. ×4.

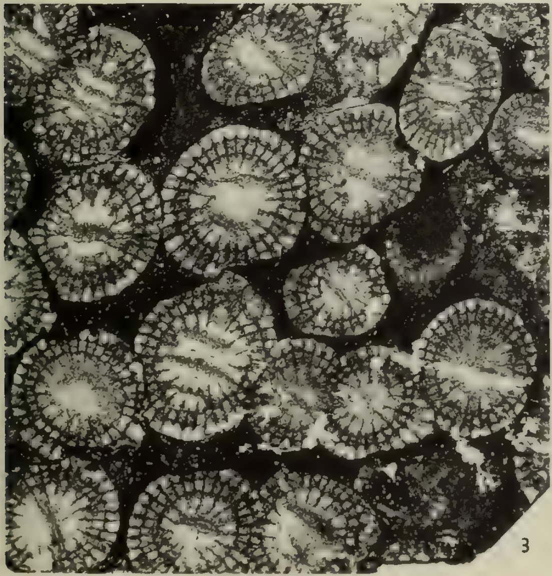
FIG. 3. Cross-section (peel). OUM D507/3/p1. ×4.

FIG. 4. Cross-section (slide). OUM D509/p1. ×4.

Figs. 3 and 4 both lower Givetian, Dyer's Quarry.


1


2


3

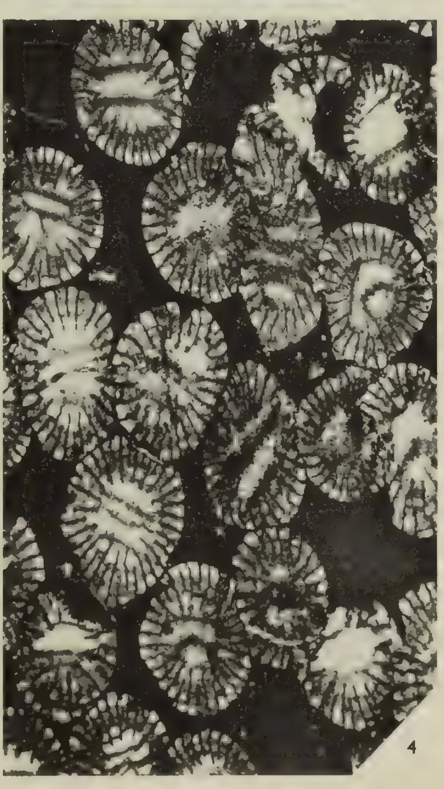
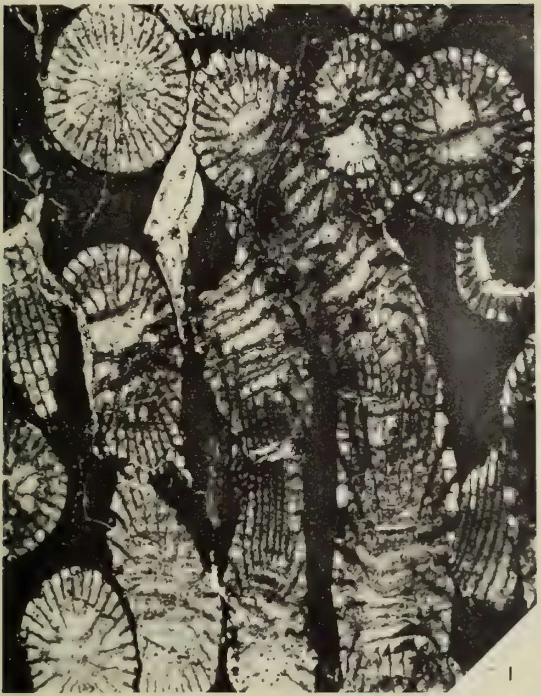
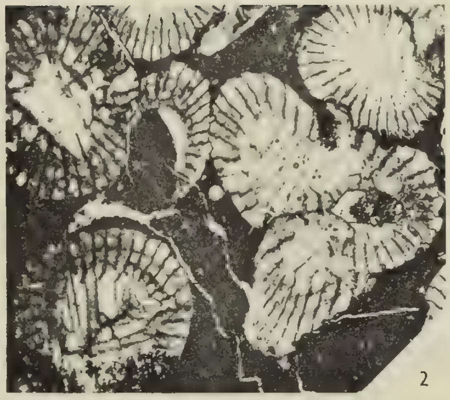

4

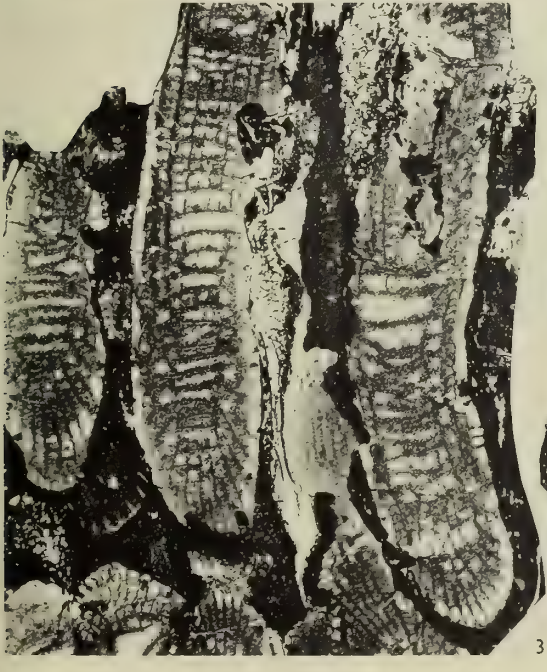
PLATE 14

Thamnophyllum germanicum schouppei nom. nov.

FIGS. 1, 2. Longitudinal- and cross-sections (slide). OUM D509/p1. ×4.
FIG. 3. Longitudinal-section (peel). OUM D507/2/p1. ×4.
FIG. 4. Longitudinal-section (peel). OUM D508/4/p2. ×4.
All lower Givetian, Dyer's Quarry.


1


2


3

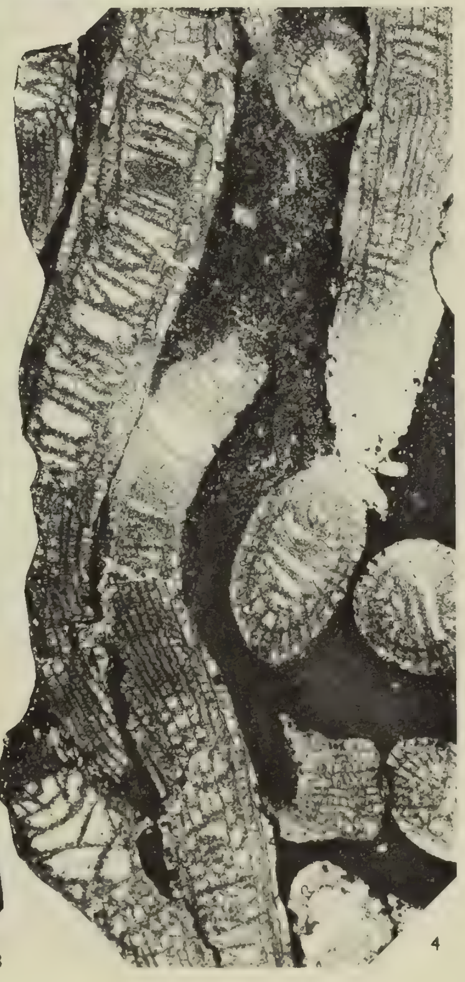

4

PLATE 15

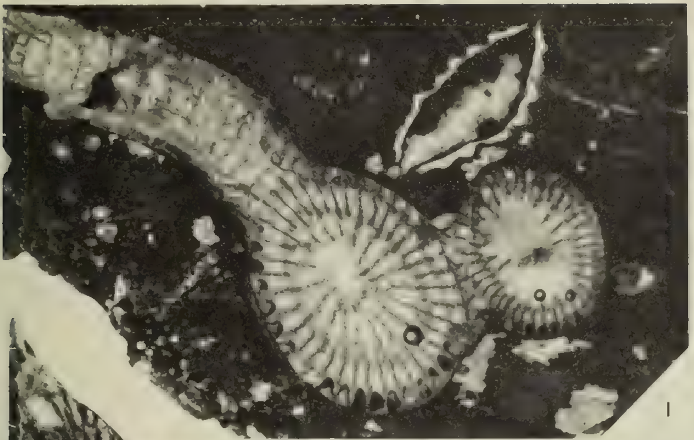
Thamnophyllum caespitosum paucitabulatum subsp. nov.

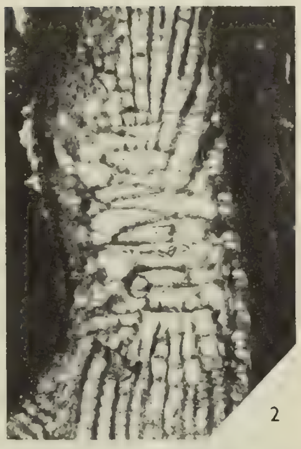
FIG. 1. Cross-section (slide). BM(NH) R46163*b*; upper Givetian, Lummaton Quarry. ×4.

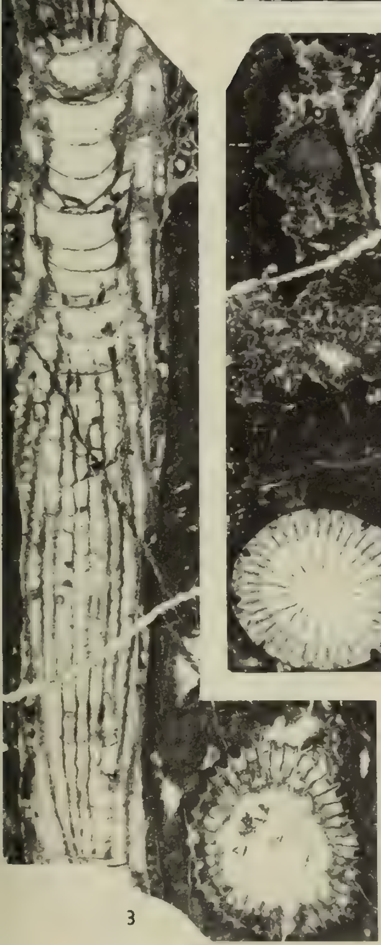
Thamnophyllum caespitosum (Goldfuss) *sensu lato*

FIG. 2. Longitudinal-section (slide). BM(NH) R46168*a*. ×4.
FIG. 3. Cross- and longitudinal-sections (slide). BM(NH) R46171*a*. ×4.
FIG. 4. Cross-section (slide). BM(NH) R46168*a*. ×4.

Figs. 2–4 all middle Givetian, Wolborough Quarry.


1


2


3

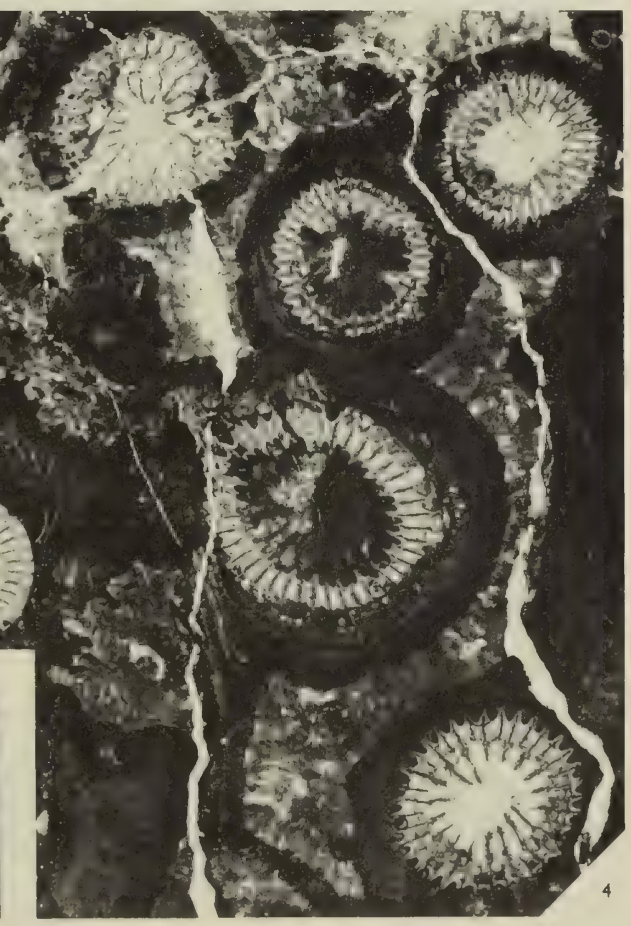

4

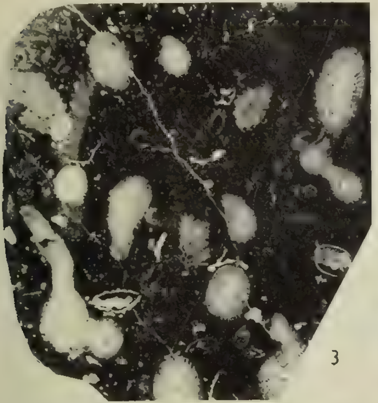
PLATE 16

Thamnophyllum caespitosum (Goldfuss) *sensu lato*

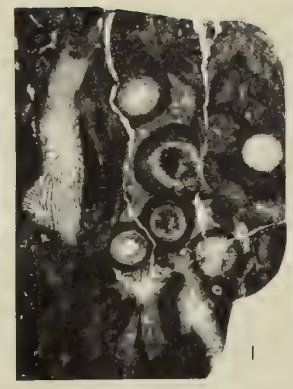
FIG. 1. Cross- and longitudinal-sections (slide). BM(NH) R46168*a*. ×1.
FIG. 2. Longitudinal-section (slide). BM(NH) R46175*b*. ×4.
Both middle Givetian, Wolborough Quarry.

Thamnophyllum caespitosum paucitabulatum subsp. nov.

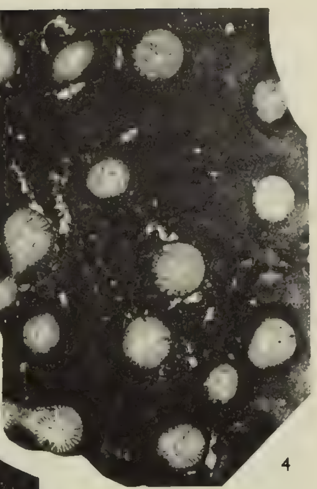
FIG. 3. Cross-section (slide). BM(NH) R46163*b*. ×1.
FIG. 4. Cross-section (slide). BM(NH) R46165*a* (cut from holotype). ×1.
FIG. 5. Cross-section (slide). BM(NH) R46165*a* (cut from holotype). ×4.
FIG. 6. Longitudinal-section (slide). BM(NH) R46165*c* (cut from holotype). ×4.
FIG. 7. Longitudinal-section (slide). BM(NH) R46165*b* (cut from holotype). ×4.
Figs. 3–7 all upper Givetian, Lummaton Quarry.



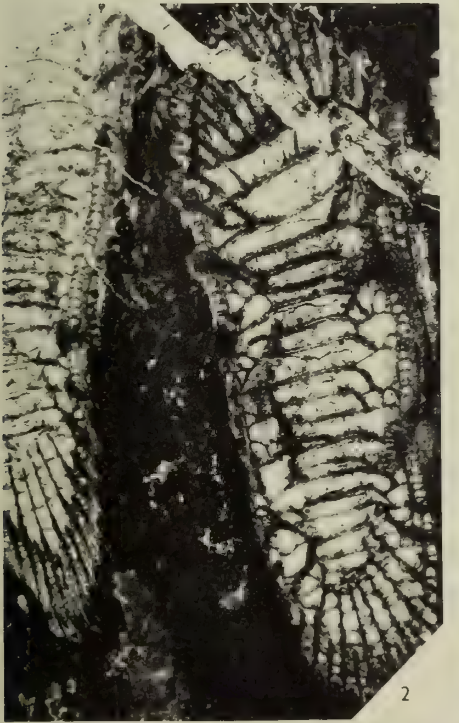
3



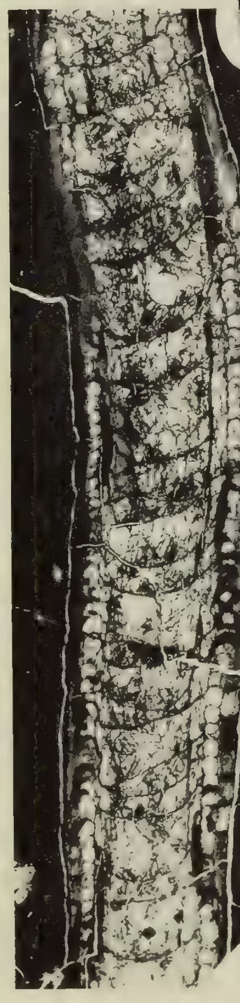
1



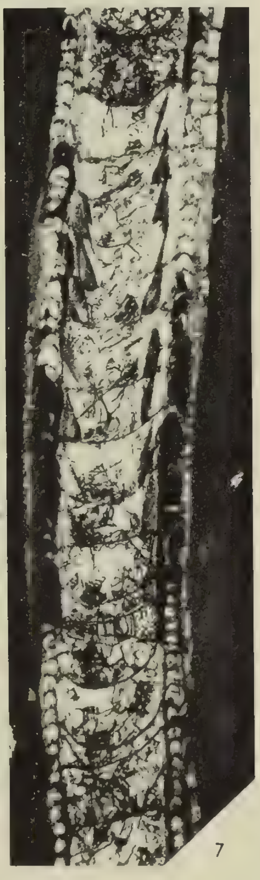
4



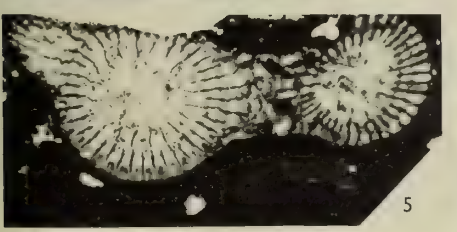
2



6



7



5

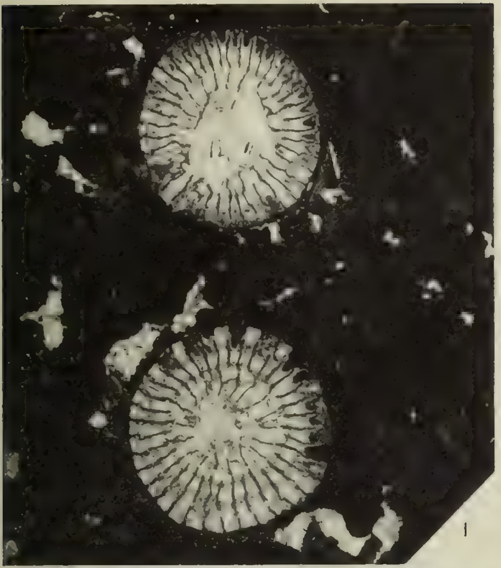
PLATE 17

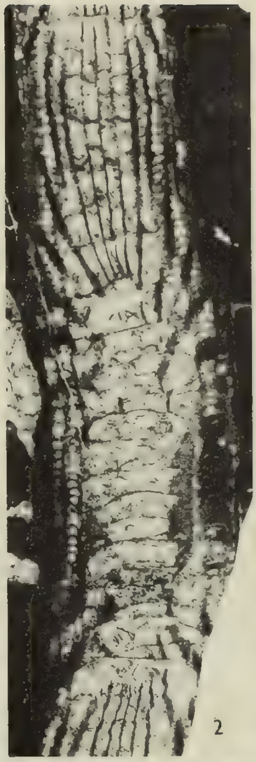
Thamnophyllum caespitosum paucitabulatum subsp. nov.

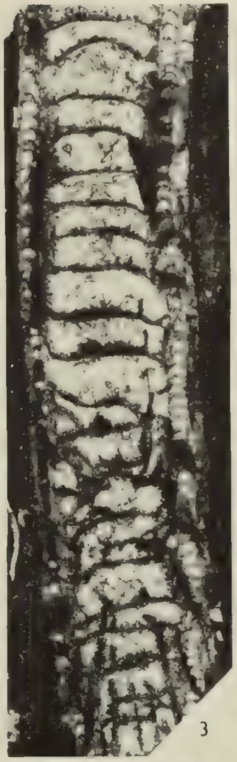
FIG. 1. Cross-section (slide). BM(NH) R46165*a* (cut from holotype). ×4.
FIG. 2. Longitudinal-section (slide). BM(NH) R46163*c*. ×4.
FIG. 3. Longitudinal-section (slide). BM(NH) R46164*d*. ×4.
All upper Givetian, Lummaton Quarry.

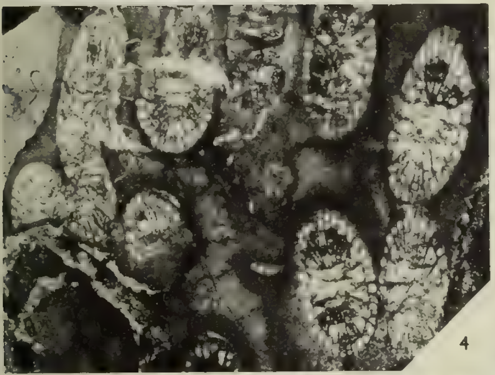
Peneckiella minor minor (F. A. Roemer)

FIG. 4. Cross-section (slide). ×3.
FIG. 5. Longitudinal-section (slide). ×6.
Figs. 4 and 5 both Bergakad. Clausthal-Z. 117 (cut from holotype); Frasnian, Winterburg near Bad Grund, Germany.


1


2


3


4

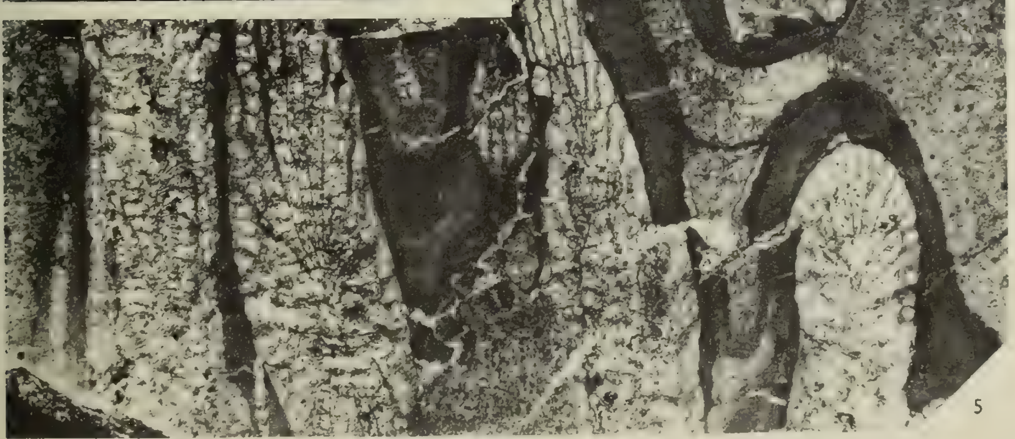
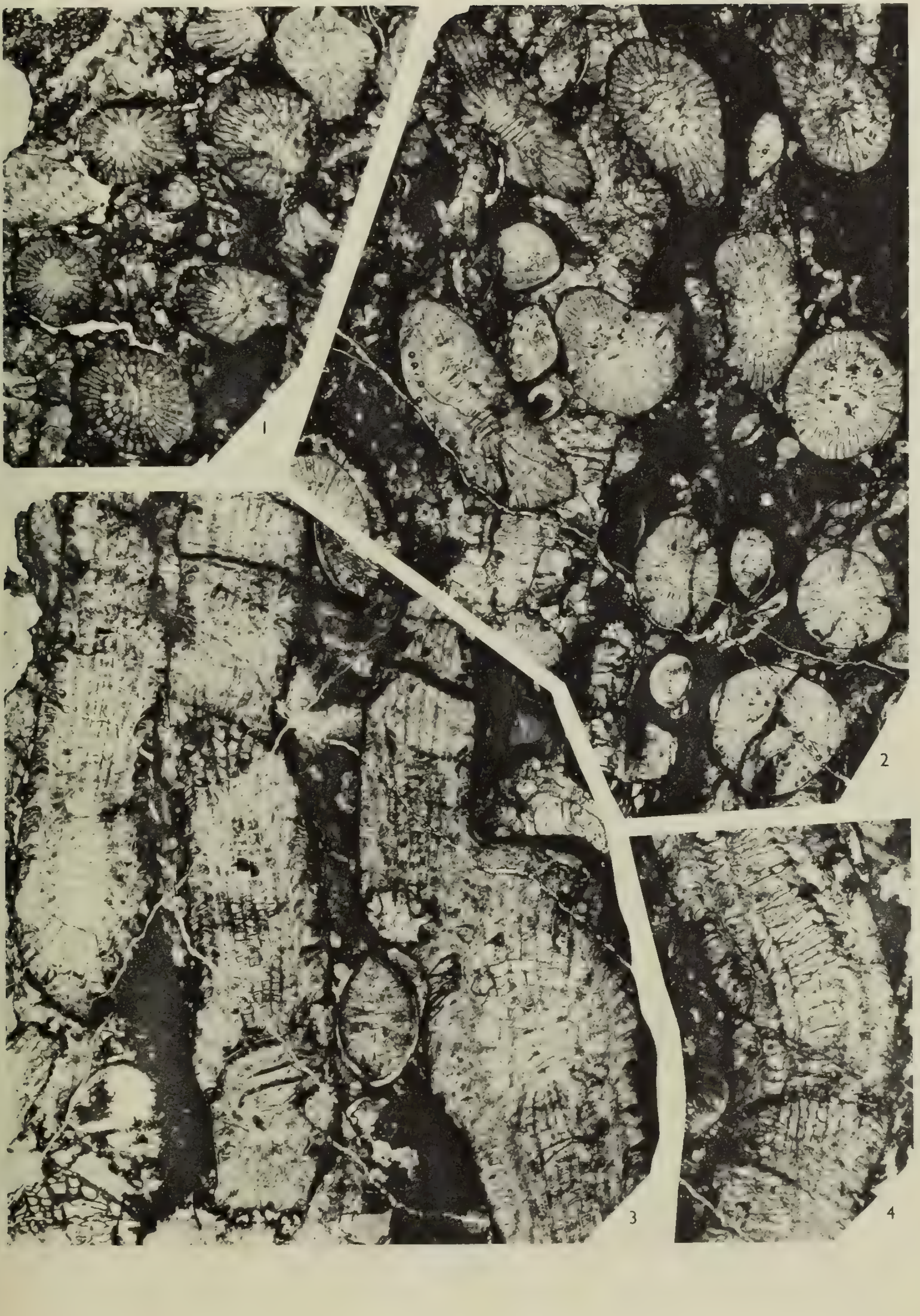

5

PLATE 18

Peneckiella salternensis sp. nov.

FIG. 1. Cross-section (slide). OUM D546/p1. ×3.
FIG. 2. Cross-section (slide). OUM D548/p1. (cut from holotype). ×3.
FIG. 3. Longitudinal-section (slide). OUM D548/p3 (cut from holotype). ×4.
FIG. 4. Longitudinal-section (slide). OUM D546/p3. ×4.

All Frasnian, main *Peneckiella* horizon, Saltern Cove.


1
2
3
4

BRITISH MUSEUM
25 MAR 1968
NATURAL HIST

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING

BRITISH MUSEUM
15 MAY 1966
NATURAL HISTORY

SOME STROPHOMENACEAN BRACHIOPODS FROM THE BRITISH LOWER SILURIAN

L. R. M. COCKS

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 6
LONDON: 1968

SOME STROPHOMENACEAN BRACHIOPODS FROM THE BRITISH LOWER SILURIAN

BRITISH MUSEUM
15 MAY 1966
NATURAL HISTORY

BY

LEONARD ROBERT MORRISON COCKS x-ref

British Museum (Natural History)

Pp. 283–324; 14 *Plates*; 1 *Text-figure*

BULLETIN OF
THE BRITISH MUSEUM (NATURAL HISTORY)
GEOLOGY Vol. 15 No. 6
LONDON: 1968

THE BULLETIN OF THE BRITISH MUSEUM (NATURAL HISTORY), *instituted in* 1949, *is issued in five series corresponding to the Departments of the Museum, and an Historical series.*

Parts will appear at irregular intervals as they become ready. Volumes will contain about three or four hundred pages, and will not necessarily be completed within one calendar year.

In 1965 *a separate supplementary series of longer papers was instituted, numbered serially for each Department.*

This paper is Vol. 15, *No.* 6 *of the Geological (Palaeontological) series. The abbreviated titles of periodicals cited follow those of the World List of Scientific Periodicals.*

World List abbreviation:
Bull. Br. Mus. nat. Hist. (Geol.).

© Trustees of the British Museum (Natural History) 1968

TRUSTEES OF
THE BRITISH MUSEUM (NATURAL HISTORY)

Issued 14 *May* 1968 *Price* £2 10s

SOME STROPHOMENACEAN BRACHIOPODS FROM THE BRITISH LOWER SILURIAN

By L. R. M. COCKS

CONTENTS

I. INTRODUCTION 286
II. SYSTEMATIC DESCRIPTIONS 286
  Superfamily Strophomenacea King 286
    Family Strophomenidae King 288
      Subfamily Strophomeninae King 289
        Genus *Pentlandina* Bancroft 289
          Pentlandina tartana Bancroft 289
          Pentlandina parva Bancroft 291
          Pentlandina parabola sp. nov. 292
          Pentlandina sp. 293
      Subfamily Furcitellinae Williams 293
        Genus *Katastrophomena* nov. 293
          Katastrophomena woodlandensis (Reed) 295
          Katastrophomena scotica (Bancroft) 296
          Katastrophomena penkillensis (Reed) 297
          Katastrophomena sp. 298
      Subfamily Leptaeninae Hall & Clarke 299
        Genus *Leptaena* Dalman 299
          Leptaena martinensis sp. nov. 302
          Leptaena haverfordensis Bancroft 304
          Leptaena valida Bancroft 305
          Leptaena urbana Bancroft 305
          Leptaena contermina sp. nov. 306
          Leptaena valentia sp. nov. 307
          Leptaena valentia mullochensis subsp. nov. . . . 309
          Leptaena zeta Lamont 309
          Leptaena reedi sp. nov. 310
          Leptaena ziegleri sp. nov. 311
          Leptaena quadrata Bancroft 312
          Leptaena purpurea sp. nov. 313
          Leptaena sp. 314
        Genus *Cyphomena* Cooper 315
          Subgenus *Cyphomenoidea* nov. 316
          C. (*Cyphomenoidea*) *wisgoriensis* (Lamont & Gilbert) . 316
          Subgenus *Laevicyphomena* nov. 317
          C. (*Laevicyphomena*) *feliciter* sp. nov. 317
        Genus *Mackerrovia* gen. nov. 319
          Mackerrovia lobatus (Lamont & Gilbert) . . . 319
        Genus *Bellimurina* Cooper 321
          Bellimurina sp. 321
III. ACKNOWLEDGMENTS 322
IV. REFERENCES 322

SYNOPSIS

The brachiopod family Leptaenidae is relegated to subfamilial rank within the Strophomenidae. All the known British Lower Silurian (Llandovery) species from the revised family Strophomenidae are described and figured. Two new genera are erected: *Katastrophomena*, type species *Strophomena antiquata* var. *woodlandensis* Reed 1917, and *Mackerrovia*, type species *Brachyprion arenaceus* var. *lobatus* Lamont & Gilbert 1945. Two new subgenera are erected within the genus *Cyphomena* Cooper 1956 (hitherto thought to be confined to the Ordovician): *Cyphomenoidea*, type species *Leptaena wisgoriensis* Lamont & Gilbert 1945, and *Laevicyphomena*, type species *C.* (*L.*) *feliciter* sp. nov. Eight new species and one subspecies are erected, and the ecological communities of all the species recorded.

I. INTRODUCTION

Three families of the superfamily Strophomenacea occur in the British Lower Silurian. One, the Stropheodontidae, has already been considered (Cocks 1967), and thus the present paper is concerned exclusively with representatives of the other two families, the Strophomenidae and the Leptaenidae.

Strophomenids are widely distributed in the Lower Silurian of Britain, but are sporadic and rare at most localities. They have been recorded under the name '*Strophomena antiquata*' in most faunal lists. Leptaenids are rather commoner and have usually been referred to '*Leptaena rhomboidalis*'. Although the Wenlock species of both families have been figured for many years, notably by Thomas Davidson in various works, the Llandovery species have remained for the most part poorly described.

The stratigraphy and correlation of the British Llandovery is at the present time under review, and a joint paper by Dr. A. M. Ziegler, Dr. W. S. McKerrow and the present author is in course of preparation. Correlation between the various areas and the type area of Llandovery itself has been effected mainly by the use of evolving brachiopod lineages such as those of *Stricklandia* (Williams 1951) and *Eocoelia* (Ziegler 1966).

II. SYSTEMATIC DESCRIPTIONS

Superfamily **STROPHOMENACEA** King, 1846

Classification

In the recent Treatise (Williams *et al.* 1965), the classification of the Strophomenacea is as follows:

- Superfamily Strophomenacea King 1846 (L.Ord.-L.Carb.)
  - Family Strophomenidae King 1846 (L.Ord.-L.Dev.)
    - Subfamily Strophomeninae King 1846 (M.Ord.-U.Sil.)
    - Furcitellinae Williams 1965 (M.Ord.-L.Sil.)
    - Rafinesquininae Schuchert 1893 (M.-U.Ord.)
    - Glyptomeninae Williams 1965 (L.-M.Ord.)
    - Oepikinae Sokolskaya 1960 (M.-U.Ord.)
    - Leptaenoideinae Williams 1953 (U.Sil.-L.Dev.)
  - Family Foliomenidae Williams 1965 (U.Ord.)
  - Family Christianiidae Williams 1953 (Ord.)
  - Family Leptaenidae Hall & Clarke 1894 (M.Ord.-L.Carb.)
  - Family Stropheodontidae Caster 1939 (U.Ord.-U.Dev.)

The Stropheodontidae is divided into seven subfamilies which are outside the scope of the present paper; the family is distinct in possessing denticles, and was held with some justification to possess superfamilial status by Sokolskaya (1960 : 213). Of the remaining families, the Foliomenidae and the Christianiidae are confined to the Ordovician, leaving the Strophomenidae and Leptaenidae to be considered here.

There is some doubt as to whether these two families are validly separable. Apart from the undiscussed list at the end of Hall & Clarke (1894 : 353–354), which divided what are now known as the suborders Strophomenidina and Triplesiidina into a rather arbitrary division between Strophomenidinae and Leptaenidae (thus creating the latter family), the two families were not divided again until 1956 in Cooper's great work on the Chazyan brachiopods. Thus Williams in his paper on strophomenoid classification (1953) did not mention the Leptaenidae: he divided the Strophomenacea into three families, the Strophomenidae, Stropheodontidae and Christianiidae, and the Strophomenidae was divided into only two subfamilies, the Strophomeninae and the Leptaenoideinae. In fact he specifically cited the Rafinesquinidae and Strophomenidae as synonymous (1953 : 8).

Cooper (1956) divided the Chazyan Strophomenacea into three families, Leptaenidae, Christianiidae and Strophomenidae. He briefly defined the three families as follows—Leptaenidae: ' Compressed to faintly lenticular Strophomenacea with large apical foramen ' (1956 : 820); Christianiidae: ' Smooth or finely costellate Strophomenacea having 4 prominent septa in the brachial valve ' (1956 : 859); and Strophomenidae: ' Strophomenacea having either normal or reversed convexity of the valves and a small foramen in the pedicle valve ' (1956 : 866). Thus, by those definitions, the only difference between a leptaenid and a strophomenid of normal convexity lies in the size of the foramen. As many species of *Leptaena* itself, e.g. *L. salopiensis* Williams, possess a foramen which is ' small, commonly sealed in adult shells ' (Williams 1963 : 461), this definition cannot be used in the type genus of the family. Even the geniculation and disc rugae may be seen on some genera, for example *Luhaia* Rõõmusoks 1956, ascribed to the Strophomeninae by Williams (1965 : H384).

However, there does occur a group of strophomenaceans which are normally geniculate and often possess rugae over most of the disc, and which may conveniently be grouped with *Leptaena* itself. But, bearing in mind the wide differences between the Strophomenidae, Christianiidae and Stropheodontidae, familial recognition as the Leptaenidae seems an unwarrantedly high taxonomic rank. In this paper they will be treated as a subfamily within the Strophomenidae, the Leptaeninae, although even this separation may not be valid, and some of the subfamilies may be inter-phyletic.

Although only three are considered in this paper, this arrangement leaves a total of seven subfamilies within the Strophomenidae, and their relative phylogenies leave much scope for discussion. Certainly the morphology of the two genera in the Leptaenoideinae, *Leptaenoidea* and *Leptaenisca*, seem to indicate descent from leptaenids rather than from other strophomenids, and this is supported by their known stratigraphical range.

Ecological occurrence

The species described in this paper are distributed as follows in the animal communities established in the British Llandovery (Ziegler 1965, Cocks 1967*a*, Ziegler, Cocks & Bambach 1968). The list omits *Leptaena urbana* Bancroft, whose community is unknown. No strophomenids have yet been found in the *Lingula* community, which is thought to have been the shallowest.

	Eocoelia Community	*Pentamerus* Community	*Stricklandia* Community	*Clorinda* Community
Pentlandina tartana Bancroft . .	—	—	×	×
Pentlandina parva Bancroft . .	—	—	—	×
Pentlandina parabola sp. nov. . .	—	—	—	×
Katastrophomena woodlandensis (Reed) .	—	—	×	×
Katastrophomena scotica (Bancroft) .	—	—	×	—
Katastrophomena penkillensis (Reed) .	—	—	—	×
Leptaena martinensis sp. nov. . .	—	—	—	×
Leptaena haverfordensis Bancroft . .	—	—	×	×
Leptaena valida Bancroft . . .	—	—	×	—
Leptaena contermina sp. nov. . .	×	×	×	—
Leptaena valentia sp. nov. . . .	—	?	×	—
Leptaena zeta Lamont . . .	—	—	—	×
Leptaena reedi sp. nov. . . .	—	—	×	—
Leptaena ziegleri sp. nov. . . .	—	—	×	—
Leptaena quadrata Bancroft . .	—	—	—	×
Leptaena purpurea sp. nov. . . .	—	—	—	×
C. (*Cyphomenoidea*) *wisgoriensis* (Lamont & Gilbert) . . .	—	×	×	?
C. (*Laevicyphomena*) *feliciter* sp. nov. .	—	—	×	—
Mackerrovia lobatus (Lamont & Gilbert)	—	—	×	—

Family **STROPHOMENIDAE** King, 1846

Apart from the Leptaeninae, there are only two groups of Strophomenidae which have so far been found in rocks of Llandovery age, as recognized by Williams (1951 : 115), who at that time referred them provisionally to *Strophomena* Rafinesque and *Holtedahlina* Foerste.

The two groups are here referred to *Katastrophomena* gen. nov. and *Pentlandina* Bancroft 1949. These are placed in different subfamilies, the Furcitellinae and the Strophomeninae, and are the only post-Ordovician genera known in either subfamily. The chief subfamilial difference (Williams 1965 : H384, H386) is that the Strophomeninae are unequally parvicostellate and the Furcitellinae are costellate, but in fact later species of *Katastrophomena* (such as *K. penkillensis* (Reed) described below) become unequally parvicostellate. Thus in the two genera concerned, the chief differences in Silurian species lie in the internal structures of the brachial valve, and the usual presence of a strong fold and sulcus in *Pentlandina*.

Subfamily **STROPHOMENINAE** King, 1846

Genus ***PENTLANDINA*** Bancroft, 1949

1949. *Strophomena* (*Pentlandina*) Bancroft : 11, 13.
1965. *Pentlandina* Bancroft Williams : H384.
1966. *Pentlandina* Bancroft; Boucot *et al.* : 25.

DIAGNOSIS: Biconvex to convexo-concave small stophomeninids with prominent fold and sulcus, often with an ornament of parvicostellae interrupting broken rugae.

TYPE SPECIES (by original designation); *Strophomena* (*Pentlandina*) *tartana* Bancroft 1949 from the Upper Llandovery of Deerhope Burn, Pentland Hills, Scotland.

Species assigned:

Strophomena (*Pentlandina*) *tartana* Bancroft 1949 : 13. Upper Llandovery, Pentland Hills, Scotland.

Strophomena (*Pentlandina*) *parva* Bancroft 1949 : 13, pl. 1, fig. 9. Upper Llandovery, The Frolic, Haverfordwest, Pembrokeshire.

Pentlandina parabola sp. nov. Upper Llandovery, Purple Shale, Shropshire.

Strophomena hirundo Barrande 1879, pl. 47, figs. 1–32 *pars*. Wenlock, Bohemia, Czechoslovakia.

Leptaena loveni de Verneuil 1848 : 339, pl. 4, fig. 5. Visby Marl (Upper Llandovery) Gotland, Sweden.

Leptaena parvula Kindle 1915 : 14, pl. 1, figs. 5–9. Stonewall Limestone, Saskatchewan, Canada.

Leptaena sinuosus Kindle 1915 : 13, pl. 1, figs. 1–4. Stonewall Limestone, Saskatchewan, Canada.

?*Leptaena lewisii* Davidson 1847 : 59, pl. 12, figs. 22–24, Lower Wenlock, Rushall Canal, Staffordshire.

DISCUSSION. *Pentlandina* was raised to generic level by Williams (1965) and placed within the Strophomeninae. Boucot *et al.* (1966) recently removed the genus to the Leptaenidae on account of the pedicle muscle field and brachial processes and adductor plates (= trans-muscle septa?). It is, however, quite impossible to agree with this point, as each of the cited structures in *Pentlandina* is firmly attributable to the Strophomeninae rather than to the Leptaeninae. In fact the morphology of *Pentlandina tartana*, the type species described below, is not like any member of the leptaeninids. Taken with a shape so typical of the subfamily, there can be no doubt that the genus lies within the Strophomeninae. *Gunnarella* Spjeldnaes 1957 has a similar ornament to *Pentlandina*, but is geniculate as opposed to biconvex and sulcate.

Pentlandina tartana Bancroft

(Pl. 1, figs. 1–6)

1868. *Strophomena antiquata* (J. de C. Sowerby); Davidson : 17, pl. 2, figs. 21–23.
1871. *Strophomena antiquata* (J. de C. Sowerby); Davidson : 299 *pars*, pl. 44, figs. 7–9 only.
1949. *Strophomena* (*Pentlandina*) *tartana* [Lamont MS] Bancroft : 13, *non* pl. 1, fig. 10.

Diagnosis: Small strophomeninid with prominent fold and sulcus. Fine ornament of differentiated parvicostellae which break irregular small weak rugae.

Description. *Exterior.* Biconvex to slightly resupinate with a semicircular outline and small ears. Large sulcus in pedicle valve with corresponding fold in brachial valve. Fine ornament of differentiated parvicostellae, and very weak irregular rugae of small wavelength distributed over all the shell. Interarea of variable size, larger in the pedicle than in the brachial valve. Large delthyrium closed at the apex by a small pseudodeltidium (Plate 1, fig. 4). Information uncertain as to the chilidium, there is at least a small one developed, but it is not clear whether or not part of the delthyrium remained open.

Pedicle interior. Straight hingeline with prominent teeth connected to the posterior end of a strong pair of short muscle bounding ridges which project anteriorly as much as dorsally. Short median septum starting close to the apex and dividing the muscle bounding ridges before stopping abruptly, leaving an inclined slope about 2 mm. long at its anterior end, which merges with the valve floor. Diductor scars short, leaving concentric growth ridges. Adductor scars elongate, close to, and partially on, the median septum. Shell thick posteriorly with prominent pseudopunctae, thin anteriorly, often with an interior reflection of the exterior ornament.

Brachial interior. Widely divergent prominent socket plates which curve slightly posteriorly at their lateral extremities. They are joined medianly to the bilobed cardinal process lobes, which are directed ventrally and slightly posteriorly. The process lobes are connected to a weak shaft, which in some specimens bifurcates anteriorly, in others reunites to form a weak median septum. Trans-muscle septa variably developed, but including in all specimens a prominent anterior pair stronger than and subparallel with the median septum. These septa are often slightly flared ventro-laterally. Owing to the mass of structures in the brachial valve presumably mainly used for the support of adductor muscles (although some could have been rudimentary brachiophore supports) the scars and shape of the muscles are not readily distinguishable. Thick shell with prominent taleolae antero-laterally.

Lectotype (here selected). BB 31447 (Plate 1, figs. 1, 2), a brachial valve in the Davidson collection. One of a number of specimens which made up the material for the composite figures cited by Bancroft. With the specimens there is a label in Davidson's handwriting '*Strophomena antiquata* Sow. bed D. Wenlock Shale, Pentland Hills, found by Mr. Henderson.' The specimens are from an horizon now known to be of Upper Llandovery age in the North Esk Inlier of the Pentland Hills, Scotland (Mitchell & Mykura 1962 : 12 *et seq.*).

Dimensions (in cm.—all specimens from type locality)

		l.	w.
BB 31447	Lectotype. Brachial valve .	0·91	approx. 1·6
B 8485	Brachial valve . . .	0·92	broken
BB 31450	Brachial valve . . .	0·86	1·39
B 13614	Pedicle valve . . .	0·72	1·29
BB 31448	Pedicle valve . . .	0·93	approx. 1·5

DISCUSSION. In erecting the species, Bancroft (1949 : 13) quoted those of Davidson's figures of *Strophomena antiquata* which came from the Pentland Hills. He also figured a specimen (Plate 1, fig. 10) which is of part of a pedicle internal mould. This specimen is not in the Sedgwick Museum and Mr. A. G. Brighton informs me (*in litt.* March, 1967) that its whereabouts are unknown. In many copies of Bancroft's privately published paper, Dr. A. Lamont has deleted reference to the figure in the species description, and substituted '*S.* cf. *penkillensis*' as the caption for Plate 1, fig. 10, and indeed the specimen is probably of the latter species and may be attributed to *Katastrophomena* of the present paper. Thus, to stabilize the identity of *Pentlandina*, Davidson's figures have been selected as lectotypes of the type species by Havlíček (1968 : 75). The original specimens used by Davidson are selected above.

Apart from the Pentland Hills, the species has not been found in form identical with the type. There is, however, a larger form, represented as yet by only one pedicle and one brachial valve, probably attributable to *P. tartana*, found in one locality in the southern Welsh Borderland. This is at Cullimore's Quarry, Charfield Green, Gloucestershire, which lies in Tortworth Beds of C_6 age, part of the Tortworth Inlier. The dimensions are as follows (in cm.).

		l.	w.
BB 31470	Pedicle valve . . .	approx. 1·3	approx. 2·2
BB 31471	Brachial valve . . .	1·39	approx. 2·3

The larger size may well be a phenotypic feature, as there seem to be no differences in ornament, internal structures or general proportions between the Tortworth and Pentland Hills specimens.

Pentlandina parva Bancroft

(Pl. 1, figs. 7, 8)

1949. *Strophomena* (*Pentlandina*) *parva* Bancroft : 13, pl. 1, fig. 9.
1951. *Holtedahlina parva* (Bancroft) Williams : 118, pl. 7, figs. 8–10.

DISCUSSION. A full description of the species is given by Williams (1951), and photographs of it are included in the present paper only for completeness and for comparison with *P. tartana* and *P. parabola*. The species is rare, it has so far been recorded only from the type locality, in Uzmaston Beds (Upper Llandovery) of the Frolic, south-west of Uzmaston Farm, Haverfordwest, Pembrokeshire. This is the same locality (Locality K of O. T. Jones on Sedgwick Museum labels) from which comes *Leptaena quadrata*, dealt with later in this paper, and it is interesting to note that neither species has been found except at the type locality.

To judge from the figures, the species seems to have a close relative in North America, the *P.* cf. *parva* of Boucot *et al.* (1966 : 25, pl. 6, figs. 16–18, pl. 7, figs. 1–10). The American species is, however, twice the size of the Welsh, no mention is made of any prominent fold and sulcus, and the arrangement of the brachial interior seems closer to *P. parabola* than to *P. parva*; all these features give a definite impression of specific difference.

Pentlandina parabola sp. nov.

(Pl. 1, figs. 9–12)

DIAGNOSIS. Alate *Pentlandina* with pronounced fold and sulcus, and two pairs of converging muscle ridges in the brachial valve.

DESCRIPTION. *Exterior.* Outline semicircular but laterally alate. A deep ventral sulcus and dorsal fold are present, but lateral to these, minor frills are sometimes developed at the valve margin. Ornament of parvicostellae, with fine threads between them, more prominently developed in the median plane. New ribs arise by intercalation. In addition, small, even concentric rugae, broken by the parvicostellae are present, forming an irregular pattern. Medium-sized interarea, with an open delthyrium, bounded laterally by plates (Pl. 1, fig. 10) and a vestigial chilidium. Very small supra-apical foramen, atrophied in adult specimens and not always on the median plane.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of muscle-bounding ridges of diamond shape, although they only sometimes meet at their anterior, enclosing a small diductor muscle scar which is weakly impressed. No information on the size and shape of the adductor muscle scars. Weak, broad median septum not extending anteriorly of the bounding ridges. Interior reflection of the ornament usually seen. Thin shell with no prominent taleolae showing.

Brachial interior. Divergent socket plates, curving antero-laterally. Small ventrally directed cardinal process lobes. Scarcely visible platform and weakly impressed muscle scars, but bounded laterally by two pairs of plates starting posteriorly at the lateral ends of the socket plates and set diagonally so that they converge anteriorly (but do not meet). Each plate is convex laterally and set at an angle to the valve floor. A very weak median septum runs for a short distance anterior of the bounding ridges.

HOLOTYPE. OUM C13507, a partly exfoliated pedicle valve from the Purple Shale (Upper Llandovery) of Domas, Shropshire. Grid Ref. SJ/5936 0062.

DIMENSIONS (in cm.—all specimens from Domas)

		l.	w.
OUM C13507	Holotype Pedicle valve .	0·89	1·70
OUM C13504	Paratype Pedicle valve .	0·68	1·22
OUM C13505	Paratype Brachial valve .	broken	1·20
OUM C13509	Paratype Brachial valve .	0·26	0·51

DISCUSSION. Length measurements were made in the median plane, but in old individuals there is some shell antero-laterally to this. In the small specimen (OUM C13509) the fold has not yet started to develop.

The species is known only from the Purple Shale of Shropshire and is rare, although it occurs as 2% of the population at the type locality. Single specimens are known from two other localities, Boathouse Coppice [Grid. Ref. SJ/6205 0398] and Devil's Dingle [Grid Ref. SJ/6392 0547].

P. parabola differs from *P. parva* (Pl. 1, figs. 7, 8) in having a still more pronounced fold and sulcus, less distinct ornament and in better differentiated alae (without, however, being more transverse). In addition the strength, proportion and arrangement of the brachial internal structures are dissimilar in the two species. From *P. tartana* the new species differs in being more apsacline, more alate, and in having a frilly margin, in having a relatively smaller total muscle area and a differently shaped socket arrangement and muscle area in the brachial valve. In addition the rugae are more prominent, the interior less strongly papillose and the whole shell less thick.

Pentlandina sp.

(Pl. 1, fig. 13)

In one block from the Bog Mine, West Shropshire [Grid Ref. SO/3510 9815], there is a single broken pedicle valve, BB 31299, which may be referred without doubt to *Pentlandina*, on its general shape, particularly its prominent sulcus, and also on the character of the muscle field and bounding ridges. It seems fairly closely related to *Pentlandina parabola* but its shell is rather more irregular; in addition no trace of the distinctive ornament may be seen, but this could possibly be due to the coarse quartzite matrix. The length is 1·02 cm. and the estimated width approximately 1·6 cm.

The specimen is significant in being the earliest representative of the genus so far known, with an age of Middle Llandovery.

Subfamily **FURCITELLINAE** Williams, 1965

Genus ***KATASTROPHOMENA*** nov.

Diagnosis. Resupinate strophomenid with an ornament of irregular subequal costellae in early stocks, but may be parvicostellate in later stocks. With dental plates and weak trans-muscle septa.

Type species. *Strophomena antiquata* var. *woodlandensis* Reed 1917.

Species assigned:

Strophomena antiquata var. *woodlandensis* Reed 1917 : 902, pl. 18, figs. 20, 21, pl. 19, figs. 1–5. Middle Llandovery, Woodland Point, Girvan, Ayrshire, Scotland.

Orthis antiquata J. de C. Sowerby *in* Murchison 1839 : 630, pl. 13, fig. 13. Wenlock Shale, Woolhope, Herefordshire.

Strophomena dura Bancroft 1949 : 15, pl. 1, fig. 11, Wenlock Limestone.

Strophonella penkillensis Reed 1917 : 900, pl. 18, figs. 11–13. Upper Llandovery, Bargany Pond Burn, Girvan, Ayrshire.

Orthis scabrosa Davidson 1847 : 61, pl. 13, figs. 14, 15. Wenlock Limestone, Benthall Edge, Shropshire.

Strophomena scotica [and var. *alveata*] Bancroft 1949 : 12, pl. 1, figs. 4–7, *non* fig. 3. Gasworks Mudstone (Lower Llandovery) Haverfordwest, Pembrokeshire.

Strophomena woodlandensis geniculata [Bancroft MS *nom nud.*] Williams 1951 : 117, pl. 7, figs. 5–7. Upper Llandovery (C_1), Llandovery, Carmarthenshire.

Strophonella costatula Hall & Clarke 1894 : 359, pl. 84, figs. 15, 16. Niagara Group, Louisville, Kentucky, U.S.A.

Strophomena radiireticulata Twenhofel 1928 : 192, pl. 17, figs. 1–3. Jupiter Formation (Upper Llandovery-Wenlock), Anticosti Island, Canada.

?Strophomena sibirica Andreeva *in* Nikiforova & Andreeva 1961 : 183, pl. 38, figs. 1–7.

Species possibly congeneric:

Strophomena rugata Lindström 1860 : 371, pl. 13, fig. 14. Visby Marl (Upper Llandovery) Gotland, Sweden. (Possibly a young strophomenid).

Strophomena? pectenoides Andreeva *in* Nikiforova & Andreeva 1961 : 184, pl. 39, figs. 1–6. Middle Llandovery, Siberian Platform, U.S.S.R.

Strophomena lindstromi Gagel 1890 : 43, pl. 3, fig. 12, Upper Silurian, east Baltic. (May be a davidsoniacean).

DISCUSSION. Unfortunately the genera of Upper Ordovician Strophomenidae have not yet been evaluated as a whole, and several are not yet comprehensively illustrated. It is probable, however, that the fairly compact group in the Silurian may be classified together in one genus to include all species not in *Pentlandina* or the Leptaeninae. All these species are resupinate and have a distinctive irregularly costate ornament, at least in the early Silurian. In addition, their internal characters, although often dissimilar at the specific level, clearly indicate their congeneric nature.

The new genus here erected to include these species is placed in the Furcitellinae, mainly owing to the similarities with *Furcitella* Cooper 1956 itself, particularly in the ornament and internal morphology, but the Chazy genus is biconvex and has a large foramen. Whether the two subfamilies Strophomeninae and Furcitellinae really require separation is another matter; the division (Williams 1965) seems to have been made mainly on ornamental grounds. In fact, although they are here left in separate subfamilies, *Katastrophomena* shows much resemblance to *Strophomena* itself in morphology, especially shape, differing mainly in the presence of dental plates and in the ornament, although, as mentioned above, *Katastrophomena* has end members with differentiated parvicostellae.

The only other strophomenid with which the new genus may be compared is *Microtrypa* Wilson 1945, from the Upper Ordovician of Ontario, Canada, which is particularly poorly known, but which appears to differ in ornament and brachial interior.

In the British Llandovery there are thus three species, *K. woodlandensis* and its subspecies *geniculata*, *K. scotica* and *K. penkillensis*, each of which will now be reviewed.

Katastrophomena woodlandensis (Reed)

(Pl. 2, figs. 1–10)

1883. *Strophomena antiquata* (J. de C. Sowerby); Davidson : 193, pl. 15, figs. 12–14.
1917. *Strophomena antiquata* (J. de C. Sowerby) var. *woodlandensis* Reed : 902, pl. 18, figs. 20, 21, pl. 19, figs. 1–5.
1949. *Strophomena woodlandensis* Reed Bancroft : 11.
1951. *Strophomena* aff. *woodlandensis* Reed; Williams : 118, pl. 7, fig. 4.

Diagnosis. *Katastrophomena* with coarse, irregular costae, variable shape, and variable brachial internal characteristics.

Description. *Exterior.* Variably resupinate, ranging from flat to almost geniculate. Ornament of thick irregular costae of subequal size. New costae arise mainly by intercalation, but sometimes by branching. Prominent growth lines seldom developed. Large interarea. Delthyrium completely closed by large pseudodeltidium and chilidium.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of muscle-bounding ridges of variable shape but which generally curve inwards without meeting anteriorly. Median septum variably developed, on either side of which are faintly impressed blade-like adductor muscle scars inside the more strongly developed diductor scars upon which may be seen both faint concentric growth lines and also radiating striae. Fairly thick shell, particularly posteriorly, but large taleolae not developed.

Brachial interior. Strong pair of widely divergent socket plates quite separate from the small erect bilobed cardinal process. Very variable minor platform and muscle area structures (compare Pl. 2, fig. 6, 8, 9). A median septum is usually present, which bifurcates to a greater or lesser degree, trans-muscle septa are occasionally present.

Lectotype, here selected. B 54490, a pedicle valve, figured by Reed (1917, pl. 18, fig. 21) from the Middle Llandovery of Woodland Point, Girvan, Ayrshire, Scotland. Gray Collection.

Dimensions (in cm.—all specimens from Woodland Point)

		l.	w.
B 54490	Lectotype. Pedicle valve .	2·17	3·01
B 73012	Brachial valve . . .	2·05	3·17
BB 31420	Brachial valve . . .	1·54	2·25
BB 31422	Brachial valve . . .	1·78	2·37

Discussion. There is a large amount of variability in *Katastrophomena woodlandensis*, particularly in two respects; the degree of valve convexity, and the development of internal brachial structures. Both points may be seen in Pl. 2; where figs. 5–7 show specimens in which the valve direction has changed in the median plane by more than 90 degrees, whereas figs. 8 and 9 show specimens which are only slightly concave. Similarly the contrast in the brachial interiors between figs. 8 and 9 is self-evident.

K. woodlandensis is not common except at the type locality, but the species is also present in the Middle Llandovery of the type area. Two specimens have been found, SMA 30006 (Williams 1951 : 118, pl. 7, fig. 4) and BB 31409, collected by the author from B_3 mudstones in a small disused roadside quarry [Grid Ref. SN/760 309].

A subspecies has also been erected, *K. woodlandensis geniculata* [Bancroft 1949 *nom nud.*] Williams (1951 : 117, pl. 7, figs. 5–7), whose type specimens are refigured here for convenience (pl. 3, figs. 1, 2). This is another rare form from C_1 beds in the Llandovery area. It is best left as a separate subspecies, as, although the brachial valve could well be identified as *K. woodlandensis* (s. s.), the form of the pedicle muscle field shows some affinity with *K. scotica* described below. Further collecting at the type locality has failed to produce more material.

The chief differences between *K. woodlandensis* and *K. scotica* are in the shapes of the pedicle muscle field and bounding ridges and in the stronger median septum usually present in *K. scotica*. The chief difference between these two species and *K. penkillensis* lies in the differentiated ornament of the latter.

Katastrophomena scotica (Bancroft)

(Pl. 3, figs. 3–9)

1871. *Strophomena antiquata* (J. de C. Sowerby); Davidson *pars* : 299, pl. 44, figs. 21, 22 only.
1949. *Strophomena scotica* Bancroft : 12, pl. 1, figs. 4, 5, *non* fig. 3.
1949. *Strophomena scotica* var. *alveata* Bancroft : 13, pl. 1, figs. 6, 7.
1951. *Strophomena scotica* Bancroft; Williams : 116, pl. 7, figs. 1–3.

DIAGNOSIS. *Katastrophomena* with irregular costae. Pedicle muscle field diamond-shaped posteriorly with bounding ridges drawing out anteriorly to become sub-parallel in extreme cases.

DESCRIPTION. *Exterior.* Variably resupinate. Ornament of thick, irregular costae of subequal size. New costae arise by bifurcation and intercalation. Prominent concentric growth-lines often developed. Large interarea, with at least a small pseudodeltidium and possibly a large, entire one. Large chilidium.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of variably developed muscle bounding ridges of curved to diamond shape, not meeting anteriorly, but sometimes drawn out and extending sub-parallel for a short distance anteriorly. Weak median septum running from the apex to approximately the ends of the muscle bounding ridges. On either side of this septum are sometimes impressed the pair of small blade-like adductor muscle scars. Strongly impressed diductor muscle scars on which concentric growth lines are often seen.

Brachial interior. Large pair of strongly divergent socket plates on either side of, and distinct from, the erect bilobed cardinal process. Between the lobes is sometimes preserved a small thin blade. Median septum usually strong, variably bifurcate. Other structures very variable, trans-muscle septa and muscle bounding ridges are sometimes weakly developed.

LECTOTYPE, here selected. SMA 32194, a pedicle internal mould, figured Bancroft (1949, pl. 1, fig. 4) from the Gasworks Mudstone (Lower Llandovery), cutting opposite entrance to gasworks, Haverfordwest, Pembrokeshire. Turnbull Collection.

DIMENSIONS (in cm.—all specimens from type locality)

		l.	w.
SMA 32194	Lectotype, pedicle valve .	2·62	approx. 3·7
SMA 32193	Pedicle valve . . .	2·46	approx. 3·5
BB 31435	Pedicle valve . . .	2·21	3·05
BB 31412	Brachial valve . . .	2·35	approx. 2·8
BB 31443	Brachial valve . . .	0·90	1·23

DISCUSSION. The second specimen figured by Bancroft has been chosen as lectotype because the first (1949, pl. 1, fig. 3) is the counterpart to the figured example of '*Strophomena*' *agrestis* from the Slade Beds (SMA 32040), and was presumably illustrated as *S. scotica* in error. Bancroft also erected a variety, *S. scotica* var. *alveata*, without giving any differences from the nominal subspecies. As the localities are the same and the types of both subspecies virtually identical (refigured here Pl. 3, figs. 4–8) and within the range of variation found in the Gasworks Mudstone, no subspecies of *K. scotica* seem necessary.

Williams (1951 : 116) selected a specimen from the Gasworks Mudstone of the Frolic section as type for the species, but as this is not one of Bancroft's originals the selection is not valid. Williams' specimen (refigured here Pl. 3, fig. 9) is, however, clearly conspecific with the type material from the entrance to the gasworks at Haverfordwest.

Katastrophomena penkillensis (Reed)

(Pl. 4, figs. 1–6)

?1871. *Strophomena antiquata* (J. de C. Sowerby); Davidson *pars* pl. 44, fig. 5 only.
1917. *Strophonella penkillensis* Reed : 900, pl. 18, figs. 11–14.

DIAGNOSIS. *Katastrophomena* with differentiated parvicostellate ornament.

DESCRIPTION. *Exterior.* Gently resupinate. Ornament of fairly fine differentiated parvicostellae, the smaller type mere threads. New ribs arise by intercalation. Large ventral interarea, but smaller on brachial valve than other species of the genus. No information on extent of pseudodeltidium. Chilidium present. Occasional prominent growth lines sometimes seen on valve exterior.

Pedicle interior. Straight hingeline with prominent teeth which form the posterior end of a pair of muscle bounding ridges of approximately diamond shape, although they do not meet anteriorly. Median septum running from the apex to a position level with, or just anterior to, the ends of the muscle bounding ridges. On either side of the anterior end of the septum are a pair of bladelike adductor scars, which themselves may run anterior to the end of the bounding ridges. Diductor scars strongly impressed, sometimes with radiating striae and concentric growth ridges. Shell of variable thickness with large postero-median taleolae not developed.

Brachial interior. Fairly straight socket plates widely divergent. Normal erect bilobed cardinal process. Variably developed muscle field structures; trans-muscle septa sometimes seen (Pl. 4, fig. 3, but not in Pl. 4, fig. 1). Broad, faint platform between two more or less circular muscle scars which are weakly impressed.

LECTOTYPE (here selected) B 73013, a brachial internal mould, figured by Reed (1917, pl. 18, fig. 11) from the Upper Llandovery of Bargany Pond Burn, Girvan, Ayrshire, Scotland. Gray Collection.

DIMENSIONS (in cm.—all specimens from Bargany Pond Burn)

		l.	w.
B 73013	Lectotype, brachial valve .	1·57	2·74
BB 31432	Brachial valve . . .	1·15	approx. 2·3
BB 31472	Pedicle valve . . .	1·40	2·86

DISCUSSION. Despite the localities being given by Reed as (1) Penkill (2) Bargany Pond Burn, all his figured specimens come from Bargany Pond Burn, where the species is, however, rare. Reed put the species into *Strophonella* as he described the hingeline as ' finely crenulated ', but there is no doubt that the hingelines of the specimens to hand, which include all Reed's syntypes, are smooth. It is surprising that Reed made this mistake, especially as Davidson had already labelled some of the specimens as *S. antiquata* (*fide* Reed 1917 : 901, no Davidson label is with the type lot today).

Katastrophomena penkillensis also occurs rarely in the higher Llandovery horizons in Shropshire, for example a pedicle valve (BB 31408) from the Minsterley Formation (pl. 4, fig. 6) and a brachial valve from the Purple Shale of the Onny River, GSM 11693.

Thus so far the species seems confined to the top half of the Upper Llandovery, and to judge both from their ornament and general aspect, it is probable that the Wenlock species of the genus were derived direct from some earlier form such as *K. woodlandensis* rather than from *K. penkillensis*, despite its wide geographical range.

Katastrophomena sp.

(Pl. 4, figs. 7, 8)

In the material from Shropshire there are, in addition to the specimens of *K. penkillensis* from the upper beds, two brachiopods referable to *Katastrophomena* from the lower horizons in the northern Longmynd-Shelve outcrop. These consist of a pedicle valve from the Venusbank Formation of The Corners, near Betton [Grid Ref. SJ/314 025] and a brachial valve from the Bog Quartzite of Bog Mine [Grid Ref. SO/3510 9815]. The latter is poorly preserved (BB 31451, Pl. 4, fig. 7), but clearly shows the furcitellinid bifurcation of the median septum. The pedicle valve (BB 31407, Pl. 4, fig. 8) is a large specimen for the genus and has a more angularly pentagonal muscle field than the contemporary *K. woodlandensis geniculata*, perhaps more similar to some specimens of *K. scotica* from the Lower Llandovery;

however the short median ridge does not extend anteriorly of the muscle bounding ridges as in the latter species.

There is no doubt as to the generic identity of these Shropshire specimens, and thus they are provisionally described here until more material comes to light. Both specimens show marked differences from the named species of *Katastrophomena*. It is noteworthy that no material ascribable to this genus has so far come to light in any part of the southern Welsh Borderland.

Subfamily **LEPTAENINAE** Hall & Clarke, 1894

The relationships and status of the leptaenids have been discussed above under the heading of the superfamily. Three genera attributable to the subfamily have been found in the British Lower Silurian, *Leptaena*, *Cyphomena* and *Mackerrovia* gen. nov. A fourth genus, *Bellimurina*, is represented by a single specimen. It is possible that some species here treated as *Leptaena* might be put into such later genera as *Bracteoleptaena* Havlíček 1963 from the Bohemian Wenlock, but in the Llandovery the variation is not enough to separate such species from *Leptaena* itself.

Genus ***LEPTAENA*** Dalman, 1828

TYPE SPECIES. *L. rugosa* Dalman 1828 from the Upper Ordovician Dalmanitina Beds of Få dalaberg, Västergötland, Sweden. A lectotype was selected and the species figured by Spjeldnaes (1957, p. 173, pl. 7, figs. 1, 2, 4), and also by Williams (1965, fig. 252, figs. 5a, 5b).

The species problem in *Leptaena* seems more acute than in most other genera of brachiopods. After the mid-Ordovician radiation, the subfamily Leptaeninae grew smaller in terms of generic numbers, and thus by Llandovery times the genera were reduced to approximately five, and all save *Leptaena* itself are rare and sporadic. On the other hand there is some variation in the form of *Leptaena* between nearly every locality in which one finds it. This bears out the assertion of Imbrie (1956, p. 219): ' Study of living populations has shown that if sufficiently rigorous methods are employed, significant morphological and genetic differences between two populations can be demonstrated. Hence species and subspecies must be considered as collective categories, in the sense that they are composed of local populations no two of which are identical.'

Thus a very large number of specific or subspecific names could have been erected in the present work, but these would have served only as a smokescreen to hide the basic truth of the ' *Leptaena rhomboidalis* ' concept. Here was a successful stock, essentially unchanged from the Ordovician to the Carboniferous, which remained firmly established in an apparent variety of ecological niches.

However there are some differences upon which species have already been erected, and in many of these cases the differences do persist in many populations from many localities. Thus their taxonomic expression is a positive step towards their recognition and understanding.

Havlíček (1968) has referred several Silurian species to *Leptagonia* on the grounds that their morphogeny has proceeded nearer that genus than to typical *Leptaena*. In this paper all the Silurian forms are retained in *Leptaena* until the Devonian and Carboniferous stocks become better known.

There now follows a list of previously erected species of *Leptaena* of Ashgill, Llandovery and Wenlock age, followed by a list of species previously referred to the genus, but which are here considered distinct from it.

Ashgill and Silurian species assigned.

Leptaena rugosa Dalman 1828 : 106, pl. 1, fig. 1. Dalmanitina Beds (Ashgill) of Västergötland, Sweden.

Anomites rhomboidalis Wahlenberg 1821 : 65. ?Wenlock of North German drift.

Producta depressa J. de C. Sowerby 1823 : 86, pl. 459, fig. 3. Wenlock Limestone of Dudley.

Leptaena tenuistriata J. de C. Sowerby *in* Murchison 1830 : 636, pl. 22, fig. 2. Wenlock of Marloes Bay, Pembrokeshire.

Leptaena depressa var. *vulgaris* Barrande 1848 : 84, pl. 22, figs. 6, 7. Wenlock/Ludlow of Bohemia, Czechoslovakia.

L. quadrilatera Shaler 1865 : 65. Ellis Bay Formation, Anticosti Island, Canada.

L. schmidti Gagel 1890 : 50, pl. 5, fig. 28. Lyckholm Fm (Upper Ordovician) East Baltic.

L. richmondensis Foerste 1909 : 211, pl. 4, fig. 10. Richmond Group, Ohio, U.S.A.

L. richmondensis var. *precursor* Foerste 1909 : 211, pl. 4, fig. 11. Richmond Group, Ohio, U.S.A.

L. rhomboidalis ' var. *β* ' Reed 1917 : 872, pl. 13, fig. 1. Whitehouse Group, Girvan, Ayrshire.

L. rhomboidalis 'var. *γ* ' Reed 1917 : 872, pl. 13, figs. 2, 3. Drummuck Group, Girvan, Ayrshire.

L. rhomboidalis ' var. *δ* ' Reed 1917 : 872, pl. 13, fig. 4. Mulloch Hill Sandstone (Lower Llandovery), Girvan, Ayrshire. (Here described as *L. valentia mullochensis*.)

L. rhomboidalis ' var. *ε* ' Reed 1917 : 872, pl. 13, figs. 5, 6, *non* fig. 7. Woodland Point (Middle Llandovery), Girvan, Ayrshire. (Here described as *L. valentia* sp. nov.)

L. rhomboidalis var. *nana* Chernychev 1937 : 67, pl. 2, figs. 16–18. Wenlock of Mongolia.

L. zeta Lamont 1947 : 200. Penkill Group (Upper Llandovery), Girvan, Ayrshire.

L. haverfordensis (and var. *contracta*) Bancroft 1949 : 6, pl. 1, figs. 18–24. Gasworks Mudstone (Lower Llandovery), Haverfordwest, Pembrokeshire.

L. valida Bancroft 1949 : 6, pl. 1, fig. 25. Upper Llandovery (C_1), Llandovery, Carmarthenshire.

L. urbana Bancroft 1949 : 6, pl. 2, figs. 1, 2. Upper Llandovery (C_4), Llandovery, Carmarthenshire.

L. elongata Bancroft 1949 : 7, pl. 1, figs. 26, 27. Upper Llandovery (C_1), Llandovery, Carmarthenshire.

L. quadrata Bancroft 1949 : 7, pl. 1, figs. 28–30. Upper Llandovery, The Frolic, Haverfordwest, Pembrokeshire.

L. ? tennesseensis Amsden 1949 : 54, pl. 5, figs. 11–15. Brownsport Formation (Wenlock/Ludlow), U.S.A.

L. delicata Amsden 1949 : 55, pl. 5, figs. 11–15. Brownsport Formation (Wenlock/Ludlow), U.S.A.

L. oklahomensis Amsden 1951 : 85, pl. 16, figs. 29–35. Henryhouse Formation (Wenlock/Ludlow), U.S.A.

L. acuteplicata Sokolskaya 1954 : 60, pl. 4, figs. 1–4. Porkuni Stage (Upper Llandovery), Estonia, U.S.S.R.

? Productus twamleyii Davidson 1848 : 315, pl. 3, fig. 1. Wenlock Limestone, Dudley, Worcestershire. [The original specimen is not now to be found, but Davidson (1871 : 282) later put the species into synonymy with *L. rhomboidalis*.]

Species excluded from Leptaena

Leptaena sinuosus and *L. parvula* Kindle 1915. See *Pentlandina*.

L. wisgoriensis Lamont & Gilbert 1945. See *Cyphomena*.

L. centervillensis Foerste 1923. Brassfield Limestone, Ohio.

L. julia (Billings 1862). See *Cyphomena*.

L. loveni de Verneuil 1848. See *Pentlandina*.

L. bella Williams 1951 : 119, pl. 7, figs. 14, 15. Middle Llandovery, Llandovery. Probably an undescribed genus, but the small amount of material at present available does not warrant redescription.

Three groups within *Leptaena* are recognizable in the British Llandovery.

(a) Large species with more or less oval-sided pedicle muscle scars.
(b) Large species with more or less parallel-sided pedicle muscle scars.
(c) Small species, which as at present known are a rather less well-knit group than either of the other two, and which will probably be found to be an amalgam of further groups when more material becomes available.

In the Lower and Middle Llandovery the first two groups of species seem to have been confined to the Scottish area and the Anglo-Welsh area respectively, and this remains substantially true for the Upper Llandovery, but in late Upper Llandovery time there was some admixture of the two groups; thus rare *L. zeta* occurs in the Purple Shale of Shropshire, and the leptaenid found in Deerhope Burn has the oval muscle-scar outline.

The first two groups could thus have shared a mutual ecological niche, as they have not so far been found occurring together. On the other hand, representatives of the third group, the small species, do sometimes occur with members of one or other of the larger groups, examples of this being at Woodland Point, Girvan, where *L. valentia* and *L. reedi* occur side by side in apparent harmony, and at locality H-G-A in the Malverns where *L. contermina* and *L. ziegleri* also occur together. Thus at least two separate ecological niches may be inferred for species of *Leptaena* in level bottom communities at this time, although for the most part only one or other of them was occupied, and the genus is absent from many localities.

Whether this scheme holds good for other parts of the world during the Lower Silurian has not yet been established. The only foreign species of *Leptaena* so far described from beds of Llandovery age, *L. acuteplicata* Sokolskaya 1954 from Estonia, has not yet been illustrated with interior views, so that its relationship with British species remains unknown.

Some consideration has been given to the possibility of formal subgeneric recognition of the three groups, but this has been withheld as taxonomic splitting of this kind does not seem justified in a generic group which remains extremely well-knit, and whose phylogeny is at the moment not completely understood, although some relationships are clear. Another possibility would be to have one species name for each of the groups, with various subspecies, but this would unite the various small forms of the third group under one specific name, which would certainly obscure the true situation, in which most of them are definitely more than subspecifically separable.

The British Llandovery species will now be described in the three groups as follows:

(a) *L. martinensis* sp. nov., *L. haverfordensis* Bancroft 1949, *L. valida* Bancroft 1949, *L. urbana* Bancroft 1949, *L. contermina* sp. nov.
(b) *L. valentia* sp. nov., *L. valentia mullochensis* subsp. nov., *L. zeta* Lamont 1947.
(c) *L. reedi* sp. nov., *L. ziegleri* sp. nov., *L. quadrata* Bancroft 1949, *L. purpurea* sp. nov.

Their possible phylogeny is shown in Text-fig. 1.

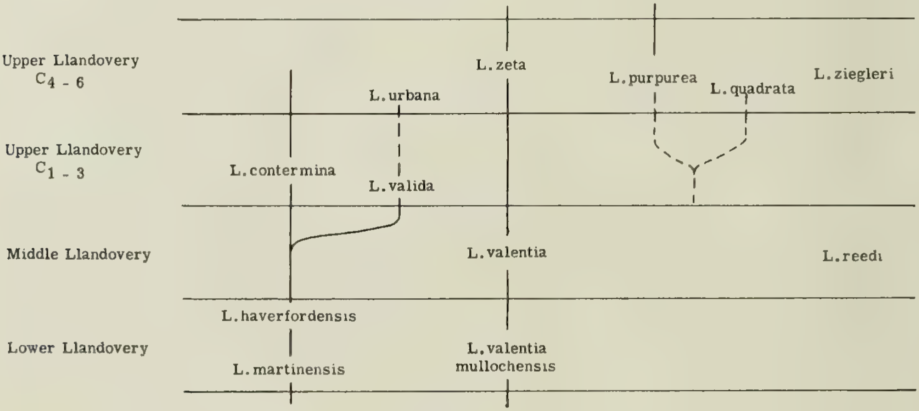

Upper Llandovery C_{4-6}
Upper Llandovery C_{1-3}
Middle Llandovery
Lower Llandovery
L.zeta
L.purpurea
L.quadrata
L.ziegleri
L.urbana
L.contermina
L.valida
L.valentia
L.reedi
L.haverfordensis
L.martinensis
L.valentia mullochensis

FIG. 1.

Leptaena martinensis sp. nov.

(Pl. 4, figs. 9–13, Pl. 5, figs. 1–3)

?1949. *Leptaena martini* Bancroft : 6, *non.* pl. 1, fig. 18 *nomen nudum.*

DIAGNOSIS. *Leptaena* with strong rugae and well defined ornament. Poorly developed muscle bounding ridges of variable shape.

DESCRIPTION. *Exterior.* Shape semicircular to quadrate with alae. Geniculation between 70 and 90 degrees. Ornament of well-defined, subequal parvicostellae. Rugae strong with a particularly large ruga at the knee. Small interarea with delthyrium mainly closed by a small chilidium. No information on the foramen, but probably small.

Pedicle interior. Widely divergent teeth with fairly prominent thin dental plates. Muscle bounding ridges are poorly developed for the genus and of variable shape, sometimes oval, sometimes angular; they do not meet anteriorly. No information on the shape of the adductor scars which are not impressed at all on the material to hand. No median septum. Central talaeolae, though not large, are more prominent than on the trail.

Brachial interior. Large divergent cardinal process lobes, mounted on a platform. The postero-lateral parts of the latter serve as the anterior ends of the sockets. The platform is trilobed anteriorly, partly enclosed subcircular adductor muscle scars. Median septum usually absent, but in a few specimens a very faint ridge may be seen about halfway to the edge of the disc. Occasional prominent pseudopunctae in the central region outside the muscle field.

HOLOTYPE. SMA 31865 a pedicle valve (both interior and exterior are preserved) from Cartlett Beds (Lower Llandovery), St. Martin's Cemetery, Haverfordwest, Pembroke. Turnbull Collection.

DIMENSIONS (in cm.—all specimens from St. Martin's Cemetery). Note that in all the following measurements of species of *Leptaena* the term l_d signifies the distance from the umbo to the knee measured along the median plane; as the trail of the various species differs so much, both in form and angle with the disc, a normal measurement of length is meaningless for comparative purposes.

		l_d	w.
SMA 31865	Holotype pedicle valve .	1·50	approx. 3·2
SMA 31859	Paratype pedicle valve .	0·62	1·22
SMA 31860	Paratype pedicle valve .	0·97	2·04
SMA 31864	Paratype brachial valve .	1·68	approx. 3·3
SMA 31861	Paratype brachial valve .	0·53	approx. 0·9

DISCUSSION. In his paper, Bancroft (1949 : 6) erected '*Leptaena martini* sp. nov.' giving St. Martin's Cemetery as the type locality, but referring the reader to his pl. 1, figs. 18, 23. These two figures are, in fact, of *L. haverfordensis* from the Gasworks Mudstone of the gasworks, Haverfordwest (SMA 32161 and 40512). Thus the species is without illustration, or reference to a previous illustration, and thus a *nomen nudum*, according to the rules of nomenclature. Bancroft mentions two species present at the St. Martin's Cemetery, a large one and a small one, but this is not borne out by the material in the Turnbull Collection or in subsequent collections made by the author. Possibly Bancroft was misled by the small individuals present in the Turnbull Collection, but these are all immature as shown by the lack of geniculation (pl. 5, figs. 1–3).

The Cartlett Mudstones are the oldest representatives of the Silurian in South Wales, and indeed almost certainly span the Ordovician-Silurian boundary, as the writer has found *Tretaspis* at their base (kindly confirmed by Dr. W. T. Dean) in a temporary (1965) exposure in the foundations for a housing estate behind St. Martin's Cemetery itself.

L. martinensis is probably an ancestor of *L. haverfordensis*, but differs from it in the more prominent ornament and rugae, and in the more variably shaped and less developed pedicle valve muscle bounding ridges.

Leptaena haverfordensis Bancroft

(Pl. 5, figs. 4–15)

1949. *Leptaena haverfordensis* Bancroft : 6, pl. 1, figs. 19–20, 23, 24.
1949. *Leptaena haverfordensis* var. *contracta* Bancroft : 6, pl. 1, figs. 18, 21–22.

DIAGNOSIS. Large *Leptaena* with oval-sided pedicle valve muscle area. Socket plates variably present.

DESCRIPTION. *Exterior.* Shape semicircular with alae. Angle of geniculation between 75 and 90 degrees. Ornament of numerous fine but well-pronounced, sub-equal parvicostellae. Well-developed regular rugae, of relatively small wave length for the genus (observed range on the pedicle valve = 10–15 in adult specimens). At the knee there is always a prominent ruga and just posterior to this an unusually pronounced trough. One or two rugae sometimes seen on the upper half of the trail. Medium-sized interarea; no information on foramen, but probably small.

Pedicle interior. Prominent teeth and dental plates merging with muscle bounding ridges of oval shape; these flare outwards from the valve floor and sometimes meet anteriorly, and sometimes are open. Prominent pair of lanceolate adductor scars between the diductor scars which often have prominent radiating striae across them. Median septum not developed except as a ridge dividing the muscles. Prominent taleolae sometimes developed centrally outside the muscle field.

Brachial interior. Prominent erect slightly divergent cardinal process lobes between widely divergent socket plates. Irregular platform developed often trilobed anteriorly to enclose the pair of suboral adductor scars. The central lobe extends further anteriorly to form a very thin, usually faint, median septum. Prominent taleolae on the disc outside the muscle field.

LECTOTYPE, here designated. SMA 32163 a pedical valve (figured Bancroft 1949, pl. 1, fig. 20) from the Gasworks Mudstone (Lower Llandovery) opposite entrance to the gasworks, Haverfordwest, Pembrokeshire.

DIMENSIONS (in cm.)

		l_d	w.
SMA 32163	Lectotype, pedicle valve .	2·21	approx. 3·5
BB 31355	Pedical valve . . .	1·60	2·96
BB 31326	Pedicle valve . . .	1·54	3·45
BB 31363	Brachial valve . . .	1·63	approx. 2·6
BB 31341	Brachial valve . . .	1·84	approx. 3·4

Discussion. Bancroft erected *L. haverfordensis* var. *contracta* from the same locality, based on a single specimen (SMA 40512) which is refigured here (Pl. 5, fig. 14). From large collections made from the Gasworks Mudstone, it is clear that there are all intergrades between this specimen, with its well impressed musculature and vascular system, and the typical form, so that no sub-species seems warranted.

The species occurs in the Lower Llandovery of Pembrokeshire and also in the type area of Llandovery, but has not yet been discovered elsewhere, which is not very surprising as these two areas represent the most fossiliferous Lower Llandovery in the Welsh area. In Girvan, the same ecological niche was occupied at this time by *Leptaena valentia mullochensis* subsp. nov.

Leptaena valida Bancroft

(Pl. 6, figs. 1–5)

1949. *Leptaena valida* Bancroft : 6, pl. 1, fig. 25.
1949. *Leptaena elongata* Bancroft : 7 pl. 1, figs. 26, 27.

Diagnosis. Large *Leptaena* with oval-sided pedicle muscle field which may be bilobed anteriorly. A few larger parvicostellae antero-medianly.

Lectotype, here selected. SMA 35690, a pedicle valve, external and internal mould (figured by Bancroft 1949, pl. 1, fig. 25) from C_1 beds (Upper Llandovery), O. T. Jones collection, his locality 26 SE/E λ13, River Sefin, 400 yards south-east of Llety'r-hyddod, Llandovery, Carmarthenshire.

Dimensions (in cm.)		l_d	w.
SMA 35690	Lectotype, pedicle valve .	1·20	approx. 4·3
SMA 35691	Pedicle valve . . .	1·83	—

Discussion. The specimen of *Leptaena valida*, one pedicle valve, and the specimens of *L. elongata*, two pedicle valves, both come from the same locality, i.e. the C_1 shales full of *Stricklandia lens progressa* by the side of the River Sefin, Llandovery. All are clearly the same species, but the lectotype has been preserved with its disc oblique to the bedding plane, and has thus been distorted to give a greater apparent width than the other two specimens. Subsequent collecting at the locality has resulted in another crushed pedicle valve, but the brachial valve is still unknown.

The species is striking in that several parvicostellae are distinctly larger than the rest in the antero-median region of the valve, giving an impression of differentiation over this small area only.

Leptaena urbana Bancroft

(Pl. 6, figs. 6, 7)

1949. *Leptaena urbana* Bancroft : 6, pl. 2, figs. 1, 2.

Lectotype, here selected. SMA 35693 a pedicle internal mould, (figured Bancroft 1949 pl. 2, fig. 1) from C_4 Beds (Upper Llandovery), O. T. Jones collection, his locality 27 NW/E λ8, quarry 500 yards north-east of Cefn Cerig, Llandovery, Carmarthenshire.

DIMENSIONS (in cm.)

		l_d	w.
SMA 35693	Lectotype, pedicle valve .	approx. 2·5	approx. 4·2
SMA 35694	Brachial valve . . .	2·25	approx. 4·5

DISCUSSION. The two specimens figured by Bancroft are the only representatives of the species in the Sedgwick Museum and further collecting from the type locality has not produced more material.

The species is distinct in its pedicle muscle field shape and size and in the weakness and irregularity of its rugae. It thus appears to have a valid specific concept, but in the absence of more material, further consideration to it will not be given here.

Leptaena contermina sp. nov.

(Pl. 6, figs. 8–13, Pl. 7, figs. 1–11)

1871. *Strophomena rhomboidalis* (Wilckens); Davidson, pl. 39, fig. 17 only.

DIAGNOSIS. Transverse *Leptaena* with interior encircling ridges in both valves, and regular rugae.

DESCRIPTION. *Exterior.* Mucronate and sharply geniculate. Apart from the large ears, the shell shape is approximately semicircular, although rather transverse. Equally parvicostellate ornament, with ribs increasing slightly in size anteriorly. Occasionally new ribs arise either by intercalation or more commonly by bifurcating (OUM C9153 shows both methods on a single brachial valve, an external mould). Rugae regular and continuous. The number of rugae on the disc varies between six and ten within a population. The geniculation occurs at different lengths within a population, but usually between 1·0 and 1·4 cm. The angle between the disc and trail is between 75 and 90 degrees. Open delthyrium, prominent chilidium. The pedicle foramen has not been observed on any specimen.

Pedicle interior. Teeth and dental plates small for the genus and fused to a small anterior extension of the hingeline. Large, prominent and evenly curving muscle boundary ridges, nearly meeting anteriorly and fusing posteriorly with an extension of the dental plates. A small median ridge divides the lanceolate adductor scars, which are usually very poorly impressed. In some specimens, the diductors completely enclose the adductors, in others they just fail to do so. Striae are developed on the muscle field, particularly on the diductors. The more coarsely pustulate disc and some of the trail are bounded by a nearly semicircular ridge which runs round the trail anteriorly but laterally crosses the geniculation and merges posteriorly with the hingeline at a low angle near the dental plates. The internal reflection of the ornament is much stronger outside this ridge. Coarse pseudopunctae posteromedianly, except on the muscle field, but not so prominent as in the brachial valve.

Brachial interior. Cardinal process lobes prominent, between them a much smaller narrow blade-like process. Socket plates variably developed and widely divergent, with rarely-preserved striae on their anterior side. Running anteriorly and laterally is a three pronged platform which bounds the posterior edge of the adductor scars, and the middle prong of which divides them, forming a short, broad median ridge. This line is marked discontinuously anteriorly as a fine ridge until near the edge of the disc, and in many specimens is more pronounced near its anterior end. As with the ventral valve a ridge runs laterally from the hingeline posterior of the sockets to the edge of the disc, but instead of crossing the geniculation as with the pedicle valve, it stays on its edge, thus making a wall on the anterior edge of the brachial valve which is not reflected on the exterior. Except in the muscle field, there are prominent pseudopunctae which are random posteriorly, but anteriorly are arranged in lines parallel to the external ornament. They are smaller and less well defined outside the encircling ridge.

Holotype. OUM C9168 a pedicle valve from the Venusbank Formation (Middle Llandovery), Hope Quarry, Shropshire. Grid Ref. SJ/3551 0208. Author's collection.

Dimensions (in cm.)

			l_d	w.
OUM C9168	Holotype, pedicle valve	Hope Quarry	1·21	2·24
OUM C9155	Paratype, brachial valve	Hope Quarry	1·11	—
OUM C10501	Paratype, brachial valve	Bog Mine	1·17	2·90
BB 31280	Paratype, pedicle valve	Bog Mine	1·34	2·81
BB 31289	Paratype, pedicle valve	Bog Mine	1·24	2·46

Discussion. There is no mistaking this species from any yet described. It is much more transverse than most species of *Leptaena*, and the rugosity is much more regular than average, yet not obscuring the ornament. As may be seen from the illustrations, there is some variation of the muscle pattern and relative dimensions, but the species is extremely homogeneous between the various localities.

Its nearest probable relative is *L. haverfordensis* from the Gasworks Mudstone, which it resembles in the general configuration of the muscle pattern (except in the strength of the adductor scars), but it does not have the raised rim to the disc of that species, nor is the rugae pattern the same. From *L. valida* and *L. quadrata* and *L. urbana*, all from the Upper Llandovery, it differs in diductor muscle configuration, rugae pattern, and also in ornament, the first two species having more prominant costellae near the median plane, and the third being almost without ornament. From the later, Wenlock, species it differs in the relative shortness and regularity of its trail, the presence of the ventral encircling ridge, and the less massive teeth and chilidium.

In Shropshire the species is confined to the Bog Quartzite and Venusbank Formation. It also occurs in the Cowleigh Park Beds of the Malverns, the Wych Beds of the Malverns and the Yartleton Beds of May Hill, the last two occurrences being substantially the younger.

Leptaena valentia sp. nov.

(Pl. 8, figs. 1–8)

1917. *Leptaena rhomboidalis* (Wilckens) var. ε Reed : 872, pl. 13, figs. 5, 6 *non* fig. 7.

Diagnosis. Large *Leptaena* with sub-parallel muscle bounding ridges.

Description. *Exterior.* Shape semicircular with more or less prominent alae. Geniculation between 70 and 90 degrees. Ornament of subequal parvicostellae, which arise by bifurcation or intercalation. Rugae fairly regular, with a particularly large ruga developed at the knee. Medium-sized interarea with prominent growth lines. Delthyrium almost entirely closed by the large chilidium, but there is a very small pseudodeltidium at the delthyrial apex. Foramen not seen, but probably small and closed.

Pedicle interior. Fairly small grooved teeth and dental plates for the genus, the latter joined to a pair of strong muscle bounding ridges which flare outwards from the valve floor. The form of the bounding ridges is variable, but they usually diverge widely posteriorly with the socket plates, then change direction sharply by up to 45 degrees becoming subparallel, continuing anteriorly until they merge with the valve floor from between half and two-thirds way to the knee. The two bounding ridges never meet. Very small median ridge on either side of which are the poorly impressed lanceolate adductor scars. The diductor muscle scars are strongly impressed within the bounding ridges and often have striae impressed upon them. Coarsely pustulate in the central region of the valve, outside the muscle area.

Brachial interior. Prominent, erect, bilobed cardinal process, the two lobes diverging slightly laterally. Immediately anterior to these is a prominent platform consisting of a pad of secondary calcite. The posterior edge of the pad on either side of the cardinal process forms the anterior edge of the sockets and has grooves to fit the teeth. The anterior edge of the pad is trilobed, forming half or more of the boundary of the roughly circular adductor muscle scars. The adductor scar area has various secondary ridges, but they are never so well developed as to form trans-muscle septa. Completely anterior of the muscle field there is usually a very fine short median septum. As with the pedicle valve the anterior is very coarsely pustulate, the individual taleolae standing up to 0·5 mm. above the valve floor.

Holotype. B 73340 a complete shell with both valves (figured Reed 1917, pl. 13, fig. 5) from the Middle Llandovery of Woodland Point, Girvan, Ayrshire, Scotland. Gray Collection.

Dimensions (in cm.—all specimens from Woodland Point)

		l_d	w.
B 73340	Holotype, pedicle valve measured	1·32	approx. 3·6
BB 55621	Paratype, pedicle valve .	1·35	2·92
BB 55637	Paratype, pedicle valve .	1·23	2·74
BB 55653	Paratype, pedicle valve .	0·98	2·24
BB 55705	Paratype, brachial valve .	1·18	2·37
BB 55706	Paratype, brachial valve .	1·25	3·60

Discussion. This species is common at the type locality, and seems to have been one of the more successful leptaenids in the Llandovery. It is clearly a direct descendant of its subspecies *L. valentia mullochensis*, described below, which inhabited the same area in the lower Llandovery. Woodland Point is also of interest in that it is one of the localities where both large and small species of *Leptaena* are found side by side, in this case *L. valentia* and *L. reedi*.

Leptaena valentia mullochensis subsp. nov.

(Pl. 8, figs. 9–15)

1917. *Leptaena rhomboidalis* (Wilckens) var. δ Reed : 872, pl. 13, fig. 4.

Holotype. B 73384, a partly exfoliated pedicle valve figured by Reed (1917, pl. 13, fig. 4) from Lower Llandovery beds, Mulloch Hill, Girvan, Ayrshire, Scotland. Gray Collection.

Dimensions (in cm.)

		l_d	w.
B 73384	Holotype, pedicle valve	1·44	approx. 3·2
BB 31375	Paratype, pedicle valve	1·24	3·34
BB 73379	Paratype, pedicle valve	0·95	1·92
BB 31386	Paratype, brachial valve	1·28	2·26
BB 31388	Paratype, brachial valve	1·29	1·94

Discussion. This form seems best considered as a subspecies of *L. valentia* as the two are very close in most morphological details, particularly in the internal structures within both valves. There are, however, various minor differences which enables Reed's separation to be confirmed. Rugae counts on pedicle internal moulds give the following results (number of rugae visible up to geniculation).

Rugae Number	*Woodland Point*	*Mulloch Hill*
4	2	0
5	18	3
6	15	8
7	2	5
8	0	2
	n = 37	n = 18

Reed (1917 : 872) noted differences between the two ' varieties ' of the angle at which the rugae meet the hingeline, but this is not supported by the present investigation. The rugae are however, less regular in *L. valentia mullochensis* than in, the typical subspecies, often being interrupted, particularly laterally.

The pedicle valve length of disc/width ratios of the two subspecies are virtually the same, having a mean of 42·8% for Mulloch Hill (n = 21, OR 31·3–57·4) and 41·9% for Woodland Point (n = 53, OR 29·0–52·8). The variability of the pedicle valve muscle field for the whole species is demonstrated by Pl. 8, figs. 10, 12, 13, 14.

Leptaena zeta Lamont

(Pl. 9, figs. 1–6)

1871. *Strophomena rhomboidalis* (Wilckens); Davidson : 281 *pars*, pl. 39, fig. 20 only.
1917. *Leptaena rhomboidalis* (Wilckens) var. ζ Reed : 872, pl. 13, figs. 8, 9.
1947. *Leptaena zeta* Lamont : 200.

Diagnosis. Very large *Leptaena* with mainly parallel-sided muscle area.

Description. *Exterior*. Shape semicircular with variably pronounced alae. Geniculation between 70 and 90 degrees, and trail proportionately shorter than is usual for the genus. Ornament of subequal parvicostellae and rugae which are usually continuous but are often irregular. Medium-sized interarea with prominent growth lines. Delthyrium mainly closed by large chilidium which appears bilobed as it wraps round the cardinal process lobes. Small foramen plugged by adventitious material.

Pedicle interior. Strong grooved teeth and widely divergent small dental plates, the latter joined to a pair of muscle bounding ridges which flare outward from the valve floor. The ridges are usually subparallel but occasionally curve inwards anteriorly, though never meeting and usually completely open (Pl. 9, figs. 2, 3). Very small median ridge sometimes developed in the muscle area between the small lanceolate adductor scars, themselves inside the strongly impressed diductor scars which often have radiating striae across them. The central area outside the muscle field is coarsely pustulate.

Brachial interior. Strong erect cardinal process lobes very close to the chilidium with faint blade between them. The lobes rest on the posterior end of a strong platform pad, which is often grooved postero-laterally to act as a socket plate. The platform anterior edge is trilobed, surrounding on three sides the pair of prominent subcircular adductor scars. A faint extension of the central platform sometimes extends further anteriorly to become a very small median septum. The central area which merges laterally with the platform is coarsely pustulate.

Lectotype, here designated. B 73355 (the original of Reed 1917, pl. 13, fig. 8), a pedicle exterior from Penkill, Girvan. Gray Collection.

Dimensions (in cm.)			l_d	w.
B 73355	Lectotype, pedicle valve	Penkill	1·97	approx. 4·4
BB 31305	Pedicle valve	Penkill	2·29	approx. 4·7
B 73364	Pedicle valve	Bargany Pond Burn	2·38	approx. 5·8
B 73365	Pedicle valve	Bargany Pond Burn	2·10	approx. 5·2
BB 31469	Pedicle valve	Minsterley Lane	approx. 2·3	6·58
BB 31468	Brachial valve	Minsterley Lane	2·05	3·42

Discussion. This is the largest species of *Leptaena* found in the British Llandovery (though not the largest in the Silurian—this is probably the undescribed species in the Woolhope limestone). It seems confined to the highest beds at Girvan—the Penkill group, and also to the Minsterley Formation of Shropshire. It is not common at any locality.

From the general aspect, particularly the shape of the pedicle and brachial muscle field, it is probably a descendant of *Leptaena valentia* sp. nov. also from the Girvan area.

Leptaena reedi sp. nov.

(Pl. 10, figs. 1–14)

1917. *Leptaena rhomboidalis* (Wilckens) var. ε (young shell) Reed : 872, pl. 13, fig. 7.

Diagnosis. Small *Leptaena*, transverse, thick shelled, with large area and pseudodeltidium.

Description. *Exterior.* Shape transverse with large alae, sometimes quadrate anteriorly. Geniculation often more than 90 degrees with the trail sometimes bending back under the disc. Ornament of subequal parvicostellae, coarser on the disc than on the trail. Symmetrical rugae on the disc, but no trace on the trail. Large interarea, particularly in the pedicle valve. Delthyrium closed partly by pseudodeltidium, partly by chilidium. Small supra-apical foramen plugged in most specimens.

Pedicle interior. Strong grooved teeth attached to a pair of distinct bilobed muscle bounding ridges which sometimes meet anteriorly, but which are sometimes divided by a small median septum. Diamond shaped adductor scars on a ridge raised between the triangular diductor scars, which are sometimes grooved. Coarse taleolae on the disc outside the muscle field. Thick shell.

Brachial interior. Erect, posteriorly directed bilobed cardinal process. Raised platform with variably developed trans-muscle septa. Short median septum sometimes developed but often absent in the muscle field. Interior reflection of rugae but not ornament. Sharp geniculation usually present, inside which is a well developed taleolae field.

Holotype. B 73341, a complete shell (figured by Reed 1917, pl. 13, fig. 7) from Woodland Point, Girvan, Ayrshire. Gray Collection.

Dimensions (in cm.)

		l_d	w.
B 73341	Holotype, pedicle valve	0·51	approx. 1·5
BB 31457	Paratype, pedicle valve	0·75	1·72
BB 31461	Paratype, brachial valve	0·68	1·81
B 73342	Paratype, brachial valve	0·66	1·38

Discussion. Reed mistook this species for the young of *L. valentia* and they occur mixed intimately (e.g. Pl. 10, fig. 10) but the two are clearly distinct in nearly every feature.

L. reedi is rare at the type locality, although the Gray Collection contains about thirty specimens, and has not been found elsewhere than at Woodland Point. Its affinities are uncertain. No other species of *Leptaena* resembles it, and the large interarea is unique amongst Silurian strophomenids. The brachial muscle field is more reminiscent of *Cyphomena* or some of the strophomenids than of other species of *Leptaena*.

Leptaena ziegleri sp. nov.

(Pl. 11, figs. 1–5)

Diagnosis. Small *Leptaena* with oval pedicle muscle field, and possessing strong socket plates.

Description. *Exterior.* Shape semicircular, occasionally quadrate with small alae. Geniculation usually at right angles. Ornament of faint subequal parvicostellae, rugae symmetrical and numerous but faint. Interarea small. Delthyrium probably mainly open, but no information on possible chilidium. Foramen not seen.

Pedicle interior. Prominent teeth and dental plates joined to strong muscle bounding ridges. The latter are of oval, almost circular shape, but not quite meeting anteriorly. Adductor scars are not seen, diductor scars are poorly impressed within the muscle bounding ridges. Faint median septum in one specimen only (OUM C4147) otherwise absent.

Brachial interior. Small, erect, bilobed cardinal process ankylosed to strong pair of socket plates. Brachial muscle field not impressed and details of muscalature not known. Very faint trace of median septum seen in some specimens only. Raised rim at edge of disc.

HOLOTYPE. OUM C4146, a pedicle valve internal mould from the Wych Beds (Upper Llandovery), Malvern Hills, Herefordshire. Grid Ref. SO/7612 3811.

DIMENSIONS (in cm.)

		l_d	w.
OUM C4146	Holotype, pedicle valve .	0·64	1·05
OUM C4147	Paratype, pedicle valve .	0·54	1·25
OUM C4137	Paratype, brachial valve .	0·58	approx. 1·9
OUM C4136	Paratype, brachial valve .	0·64	approx. 1·4

DISCUSSION. The species is known only from its type locality. It is distinctive in pedicle and brachial internal structures and in its shape and ornament. The species is named after Dr. A. M. Ziegler, who collected the material.

Leptaena quadrata Bancroft

(Pl. 11, figs. 6–10)

1949. *Leptaena quadrata* (Reed MS) Bancroft 1949 : 7, pl. 1, figs. 28–30.

DIAGNOSIS. Small quadrate *Leptaena* with many fine rugae.

DESCRIPTION. *Exterior.* Shape quadrate with small but pronounced alae. Small trail after geniculation of approximately 80 degrees. Ornament of fine symmetrical rugae and faint subequal parvicostellae. Interarea of average size. No information on possible pseudodeltidium; small chilidium present. Foramen not known, but probably small.

Pedicle interior. Small divergent teeth joined to variably developed muscle bounding ridges. The latter are long and sub-parallel, sometimes merging anteriorly with the valve floor (Pl. 11, fig. 6), sometimes swinging round in an irregularly bilobed fashion (Pl. 11, fig. 10). A pair of elongate adductor scars between the impressed long diductor scars. Median septum absent.

Brachial interior. Erect bilobed cardinal process. Weak platform posteriorly acting as socket plates, anteriorly enclosing weakly impressed adductor muscle field of approximately oval shape. Sometimes very thin median septum weakly developed.

LECTOTYPE, here selected. SMA 32437 a pedicle valve internal and external mould (figured Bancroft 1949, pl. 1, fig. 28) from Uzmaston Beds (Upper Llandovery),

O. T. Jones Collection, 'locality K, below path south west of Uzmaston,' The Frolic, near Haverfordwest, Pembrokeshire.

DIMENSIONS (in cm.)		l_d	w.
SMA 32437	Lectotype, pedicle valve .	0·73	0·86
SMA 32444	Pedicle valve . . .	0·55	0·86
SMA 32438	Brachial valve . . .	0·63	1·02
SMA 32441	Brachial valve . . .	0·53	0·93

DISCUSSION. This species is known only from its type locality where it occurs in a slightly crushed greenish siltstone. Its associates are *Amphistophia whittardi* Cocks, *Pentlandina parva* Bancroft, *Dicoelosia* cf. *alticavatus* (Whittard & Barker), *Coolinia* sp., *Atrypa* sp., *Eospirifer* sp. and *Eoplectodonta millinensis* (Jones), which indicate on balance a *Clorinda* community, although no pentamerids have been seen.

The usual leptaenid in the Welsh Borderland *Clorinda* community is *L. purpurea* sp. nov., and Bancroft's species may be related to it. *L. purpurea* has, however, a completely different muscle field disposition in both pedicle and brachial valves, and different overall proportions. It is also larger.

Leptaena purpurea sp. nov.

(Pl. 12, figs. 1–6)

1932. *Leptaena* sp. nov. Whittard, table facing p. 896.

DIAGNOSIS. Small quadrate *Leptaena* with usually oval-sided pedicle muscle bounding ridges.

DESCRIPTION. *Exterior.* Shape quadrate with small ears. Sharply geniculate with approximately a right angle between disc and trail, but the angle varies between obtuse and acute. Ornament of fine, subequal parvicostellae, with new costellae arising by intercalation. Rugae cover the whole disc on both valves; they are fairly regular and have a small wavelength. Small external rim on the ventral knee and a small groove on the dorsal knee. Open delthyrium, large chilidium, but rather smaller interarea than is common for the genus. No information on the pedicle foramen, except of a very young specimen (OUM C13141) in which it is supra-apical and probably, at that stage, functional.

Pedicle interior. Straight hingeline with open delthyrium flanked by relatively large dental plates, considering the small size of the species which are combined in part with a raised posterior extension of the muscle bounding ridges. Faint muscle grooves often seen on the muscle field. Diductor scars bilobed and surrounded laterally by pronounced bounding ridges which in some specimens curve round anteriorly to form an ω shape, although they do not quite meet in the centre. Small lanceolate adductor scars, though seldom seen, are separated by a fine median ridge which in a few specimens continues anteriorly of the muscle bounding ridges. In completely preserved specimens there is a ridge running about half-way down the trail and nearly all the way round it, but postero-laterally crossing the geniculation and merging at a low angle with the hingeline, although on many specimens the ridge is very faint. Pseudopunctae coarse near the umbo, except where absent in the muscle field. They are apparently randomly distributed near the umbo, but antero-laterally they tend to be arranged in lines parallel to both the rugae and the ornament.

Brachial interior. Raised cardinal process with two stout lobes directed ventrally. Large chilidium fused close to the base of the cardinal process. Anchor shaped platform present, the haft of which forms a median ridge dividing the two pairs of oval adductor muscle scars, which are separated from each other by the pair of low short ridges running laterally from each side of the haft. Disc surrounded by raised rim, which is reflected to a lesser extent by the exterior groove, indicating a local thickening of the shell material. Mantle canals visible occasionally (Pl. 12, fig. 3) coming from the floor of the disc, up over the rim and fading towards the valve margin. No bifurcations seen. Pseudopunctae very noticeable postero-medianly, but scarcely visible on rim or trail.

HOLOTYPE. BB 31465, a pedicle internal mould from the Purple Shale (Upper Llandovery) of Domas, Shropshire. Grid Ref. SJ/5936 0062.

DIMENSIONS (in cm.).

			l_d	w.
BB 31465	Holotype, pedicle interior	Domas	0·52	1·06
BB 31466	Paratype, brachial interior	Hughley	0·51	1·19
OUM C12062	Paratype, pedicle interior	Onny River	0·54	1·08
OUM C13480	Paratype, brachial exterior	Domas	0·43	1·15
OUM C13478	Paratype, brachial exterior	Domas	0·47	1·21
OUM C13477	Paratype, brachial exterior	Domas	0·45	1·20
OUM C13482	Paratype, pedicle interior	Domas	0·41	0·79
OUM C13141	Paratype, brachial exterior	Wall-under-Heywood	0·20	0·29

DISCUSSION. Although leptaenids are to be found in nearly every collection from the Purple Shales, they are never common, but those that do occur are usually attributable to this form. The species is small, and thus only strictly comparable with *L. quadrata* Bancroft from the Upper Llandovery of the Frolic, Haverfordwest, from which it differs in its larger teeth, encircling muscle ridges and the character and strength of the rugae.

One specimen of a leptaenid of comparable size, 1·35 cm. wide, has been collected (Bristol University Museum 12101) from the contemporary Damery Beds (C_5) of Tortworth by Dr. M. L. K. Curtis. The specimen, a pedicle valve (Pl. 12, fig. 6), differs from *L. purpurea* in the indented shape of the muscle bounding ridges and also in the almost complete absence of internal ornament or rugae, but in general shape and size it is similar. Without further material, particularly brachial valves, any definite attribution seems unwarranted.

***Leptaena* sp.**

(Pl. 12, figs. 7, 8)

EXTERIOR DESCRIPTION. Shape quadrate and alate. Ornament of subequal, fine parvicostellae. Small rugae, uneven round the disc, but giving the illusion of not being so. At least eighteen rugae of subequal wavelength (except near the umbo) on the ventral disc and sixteen on the dorsal. Geniculation less than right angles on the ventral valve, but the trail curves into a steeper angle, meeting the anterior margin at an acute angle with the disc. Small external rim on the ventral knee, and small external groove on the dorsal knee. Prominent interarea. Open delthyrium, large chilidium, with growth-lines persisting to the interarea. Small foramen about 0·2 mm. diameter.

Locality. Purple Shales, ' near Harley ', Shropshire.

Dimensions. width = 3·6 cm. approx., length = 1·73 cm., length of disc = 1·43 cm., height of trail = 1·2 cm.

Discussion. In the late Professor Whittard's collection there is one complete specimen (BB 31467) of *Leptaena* which cannot be assigned with confidence to any described species, but until interior details are known, to name a new species would be premature. Though too big for *Leptaena purpurea* it is sufficiently close to it for the possibility of a sport not to be ruled out completely, despite its large disc and overall size. Its shell thickness, interarea, and general proportions are much finer and more delicate than the Wenlock *L. depressa*. It may, however, be related to a large, undescribed species of *Leptaena* present in the Woolhope Limestone of Crickley Common, Herefordshire and elsewhere.

Genus ***CYPHOMENA*** Cooper 1956

Type species. *Leptaena homostriata* Butts 1942 from the Oranda Formation (Middle Ordovician) of Virginia, North America.

Discussion. When Cooper (1956 : 840) erected *Cyphomena* he put into it three species (and tentatively a fourth), all from the Middle Ordovician of North America. Subsequently Williams (1962 : 203) recognized one of them in the Scottish Caradocian. These are the only published records.

The interior disposition and external form of the various species of *Cyphomena*, so well figured by Cooper, leave no doubt of the close relationship between them and some species present in the Llandovery. In particular the gradually curving pedicle valve and sharply geniculate brachial valve, the proportions and disposition of the musculature and denticulation in both valves, and the small curved pseudodeltidium not completely filling the delthyrium, above which is developed a sufficiently large pedicle foramen for it to be considered functional, are identical in Ordovician and Silurian specimens.

There is, however, one point of difference in that Cooper's genus ' never developed the concentric wrinkling of the visceral region ' (1956 : 841). It is true that complete rugae of the type found in *Leptaena* are not seen in the Silurian forms, but interrupted, sometimes zig-zag, rugae between the costellae are often well-developed, for example in *C. wisgoriensis*. This is in contrast to the simple costellae of the Caradocian species. This zig-zag type of ornament occurs many times in the Strophomenida and must be polyphyletic, perhaps the best-known example being the plectambonitacean *Ptychoglyptus*. In addition there occurs in the Llandovery a form, described below, which apparently lacks ornament of any kind, but has interior and general form very close to the Ordovician species.

Thus to satisfactorily represent the close relationship between all these forms, but also to bring out their inherent differences, two new subgenera of *Cyphomena* are proposed here, one, *Cyphomenoidea*, to include forms with interrupted rugae, and the other, *Laevicyphomena*, to include forms, only one of which is at present known, which lack exterior ornament of any kind.

***CYPHOMENA* (*CYPHOMENOIDEA*) subgen. nov.**

Diagnosis. *Cyphomena* with parvicostellate ornament, the major ribs interrupting small, irregular rugae over the whole shell.

Type species. *Leptaena wisgoriensis* Lamont & Gilbert 1945.

Range. Llandovery, ?Wenlock Series.

Discussion. The same type of ornament as appears on *Cyphomenoidea* may also be seen on many species of *Pentlandina*, for example the contemporaneous *Pentlandina loveni* (de Verneuil 1848) from the Visby Marl of Gotland. It is seen again on *Strophomena julia* Billings 1862 from the Jupiter Formation (Upper Llandovery) of Anticosti Island, Canada, but in this case illustrations of the interior are not available. A topotype in the British Museum (B 76891), a complete shell with both valves joined, has the correct profile for the new subgenus, but the species may be a strophomeninid and cannot be referred to *Cyphomenoidea* with confidence until the interior is known.

Cyphomena* (*Cyphomenoidea*) *wisgoriensis (Lamont & Gilbert)

(Pl. 12, figs. 9–12)

1945. *Leptaena wisgoriensis* Lamont & Gilbert : 660, pl. 3, figs. 10–14.
1951. *Leptaena wisgoriensis* Williams : 119.

Type locality. Sunken track through Coneygore Coppice, near Alfrick, Worcestershire [Grid Ref. SO/7464 5111].

Discussion. A full description of the species may be found in Lamont & Gilbert (1945 : 660–662). Although a large collection in the Oxford University Museum by Dr. Ziegler from the type locality failed to produce specimens of *C. wisgoriensis*, good material was found at Grid Ref. SO/7430 5152, less than a third of a mile away and at the same stratigraphical horizon, and some is illustrated here. A comparison of Pl. 12, fig. 10 with pl. 224, fig. 21 of Cooper (1956) reveals that the interior of the brachial valves of *C. wisgoriensis* and *C. angulata* Cooper are virtually identical, apart from the smaller size, more pronounced reflection of the ribbing (or possibly pallial sinuses) and slightly larger anterior median ridge of the latter species. In particular the distinctive shape of Cooper's species, with a sharp geniculation and raised rim in the brachial valve and much more gentle curve without geniculation in the pedicle valve, together with the close similarity of internal structures in both valves, pronounce them to be close relatives.

The major difference between the two lies in the nature of the ornament, as mentioned in the discussion of the genus. All three species described by Cooper have more or less equally costellate ornament, whereas *C. wisgoriensis* has a subequal parvicostellate ornament, upon which is superimposed small irregular rugae separated from each other by the larger ribs, forming a regular zig-zag pattern (Pl. 12, fig. 12).

The species has been recognized only from the Wych Beds (C_{5-6} in age) of the North Malverns and Ankerdine Hill, but a solitary external mould of a brachial valve from the Purple Shale of Hughley, Shropshire, has a similar ornament and may tentatively be referred to *C. wisgoriensis*.

CYPHOMENA (LAEVICYPHOMENA) subgen. nov.

DIAGNOSIS. *Cyphomena* with no shell ornament.

TYPE SPECIES. *Cyphomena (Laevicyphomena) feliciter* sp. nov.

RANGE. Middle to Upper Llandovery Series.

DISCUSSION. The new subgenus has as yet only one species attributed to it. Although it is fairly certain that the latter has no ornament, it has admittedly been found so far only in sandstone matrices, and it is possible that some sort of very fine ornament might have escaped detection.

Cyphomena (Laevicyphomena) feliciter sp. nov.

(Pl. 12, figs. 13–14, Pl. 13, figs. 1–9)

1932. *Stropheodonta funiculata* (M'Coy); Whittard *pars*, table facing p. 896.

DIAGNOSIS. Smooth *Cyphomena* with laterally concave ridges in the brachial valve.

DESCRIPTION. *Exterior.* Shape trapezoidal, varying sometimes to semicircular, particularly in the outline of the brachial geniculation. Sometimes slightly alate. Pedicle valve has a gradual convexity, always less than a total of 90 degrees, but brachial valve flat apart from its geniculation. No visible ornament, but fine growth-lines have been observed on the trail only of a few specimens, and the shell surface may be slightly buckled (rugate would be too definite a term) near the lateral extremities only. Interarea medium-sized to small for a leptaenid. Small chilidium. Functional foramen at apex of pedicle valve, below which is a small pseudodeltidium apparently not entirely covering the delthyrium.

Pedicle interior. Thickened hinge line, the anterior edge of which diverges laterally away from the umbo until it reaches the edge of the trail, where it thins and becomes flush with the main shell. Prominent dental plates (but short in a dorsal direction) diverge at an angle of 90 degrees or more, and continue anteriorly as muscle bounding ridges which persist for a short distance in the same direction, but then swing through an angle of 60–80 degrees to converge again, though they do not meet. Thus the pedicle muscle field is somewhat similar to that of a strophomeninid, except when the species becomes gerontic (Pl. 13, fig. 7), and an anterior fold connects the two bounding ridges, overriding the median septum which in young specimens divides them. Rarely (e.g. Pl. 13, fig. 1) the muscle field presents a rather more bilobed appearance, with the median septum poorly developed except anteriorly. No trace of pseudopunctae seen.

Brachial interior. Straight hinge line, to which is fused a pair of widely divergent socket plates. Two small cardinal process lobes approximately at right angles to the valve floor. Small platform, ending anteriorly with a very short, small median ridge, a trace of which may often be seen again in the anterior part of the disc, although it is never continuous. From approximately the antero-lateral end of the socket plates, and usually separated from them by a short gap, run a pair of ridges, subparallel to the median plane but concave outwards. The degree of concavity varies, and a small proportion are almost straight. These ridges bound the anterior pair of adductor muscle scars, which are particularly elongate. The posterior pair are smaller, approximately round, and situated immediately anterior of the socket plates. They are occasionally separated from the anterior adductors by two poorly-developed small nodes, which are just posterior of the point of closest proximity of the two bounding ridges. The geniculation is sharp (in contrast to the pedicle valve) and often associated with a marked interior rim, which is not reflected on the exterior. No trace of pseudopunctae observed.

HOLOTYPE. BB 31346, a pedicle valve from the Bog Quartzite of Bog Mine, Shropshire [Grid Ref. SO/3510 9815]. Other localities (all in Shropshire): Napp Outlier [SO/3493 9922], Josey's Wood [SJ/3653 0221] and Bank Outlier [SJ/3821 0418].

DIMENSIONS (in cm.)

			l	w.
BB 31346	Holotype, pedicle valve	Bog	0·62	1·45
BB 31345	Paratype, pedical valve	Bog	0·74	2·02
OUM C9895	Paratype, pedicle valve	Bog	0·70	1·40
OUM C10988	Paratype, pedicle valve	Josey's Wood	0·78	1·52
BB 31348	Paratype, brachial valve	Bog	0·71	1·96
OUM C9893	Paratype, brachial valve	Bog	0·68	—
BB 31347	Paratype, brachial valve	Bog	0·69	1·61
BB 31352	Paratype, brachial valve	Napp Outlier	0·71	1·71

DISCUSSION. It is unfortunate that this distinctive species should be preserved only in fairly coarse matrices, so that fine details of possible ornament or arrangement of pseudopunctae cannot be observed. So far the species is confined to the Bog Quartzite and Venusbank Formation of Shropshire; only two specimens (OUM C10988 from Josey's Wood and BB 31354 from Bank Outlier) have been recovered from the latter horizon, and the species does not occur above 1 % in any collection.

C. feliciter is not far removed from *C. wisgoriensis* and other older species of *Cyphomena*, but differs from them in many ways—the lack of distinctive ornament, the development of the brachial ridges, and the general proportions and shape of the valves. However there are sufficient characteristics in common, particularly the general internal arrangement, the open foramen and small pseudodeltidium, and the geniculation angles in both valves, to enable the new species to be included in *Cyphomena* with a fair degree of confidence.

Genus ***MACKERROVIA*** nov.

DIAGNOSIS. Irregularly geniculate leptaenid with long diductor scars in the pedicle valve, bounded laterally by high irregular ridges, and partially mirrored in the brachial valve by long anterior adductor scars, bounded by less pronounced ridges. Shell surface often irregular. Very faint, often invisible ornament of differentiated parvicostellae. Pedicle atrophied in adults.

TYPE SPECIES. *Brachyprion arenaceus* var. *lobatus* Lamont & Gilbert 1945 emended below, the only known species.

DISCUSSION. *Mackerrovia* is quite different from any genus yet described, and its attribution to the leptaeninids rather than to any other subfamily within the Strophomenidae is based mainly upon the geniculation. The most distinctive feature is the long muscle scars bounded by high ridges in the pedicle valve (and corresponding traces in the brachial valve). This is paralleled only by a homoeomorphic development in the Stropheodontidae, namely *Shaleria* and to a lesser extent some species of *Amphistrophia*, but in these genera the ridges are much more uniform. The present genus is not a stropheodontid, despite its previous ascription to *Brachyprion*, and the whole internal structure is quite different, in addition to there being no trace of denticles on the hingeline. As well as possessing the long scars, *Mackerrovia* differs from other leptaeninid and strophomeninid genera in the usual absence of rugae and also the highly irregular shell surface, which is more reminiscent of some Upper Palaeozoic davidsoniaceans.

The genus, known so far only from the higher part of the Upper Llandovery in the Welsh Borderland, is named after Dr. W. S. McKerrow.

Mackerrovia lobatus (Lamont & Gilbert)

(Pl. 13, figs. 10–15; Pl. 14, figs. 1–8)

1871. *Strophomena arenacea* [Salter MS] Davidson *pars*, pl. XLII, figs. 7–8, *non* fig. 6.
1945. *Brachyprion arenaceus* var. *lobatus* Lamont & Gilbert : 667, pl. VI, fig. 6, pl. VII, fig. 2.
1945. *Brachyprion arenaceus* var. *geniculatus* Lamont & Gilbert : 669, pl. VI, figs. 1–5, pl. VII, fig. 3.
1953*a*. *Brachyprion arenaceus* var. *geniculatus* Lamont & Gilbert; Williams : 23.

DIAGNOSIS. As for genus.

DESCRIPTION. *Exterior.* Shell shield-shaped with no alae. More or less sharp geniculation occurs at a variable length (occasionally, e.g. Pl. 13, fig. 15, two geniculations are visible). Shell surface uneven and irregular in detail. Some specimens show well-developed growth lines. Ornament of extremely faint parvicostellae with even smaller stripes between them, but this is not seen on most specimens. Hingeline straight, but immediately anterior to it the shell often curves up (viewed from the posterior) from the umbo. Pseudodeltidium closes the delthyrium flush with the interarea, the latter being of variable size and sometimes scarcely developed at all in the brachial valve. No trace of a foramen observed.

Pedicle interior. Thickened hingeline with medium-sized teeth that protrude anteriorly as well as ventrally. Long diductor muscle scars are of irregular shape and enclose long adductor scars separated by a small but persistent median ridge. Round the scars, posteriorly as an extension of the teeth, are long, high bounding ridges of variable shape, subparallel, concave or convex, or a mixture of the three. Sometimes they converge anteriorly (Pl. 14, fig.1), sometimes they diverge (Pl. 14, fig. 7). They usually double back round the anterior end of the diductors, but are always prevented from meeting by the median ridge. Usually the bounding ridges are not at right angles to the valve floor, but are directed dorso-laterally. The whole muscle area is not always in the median plane, and may be directed anteriorly either to right or left. Fairly large pseudopunctae visible on most specimens everywhere except on the muscle field.

Brachial interior. Prominent cardinal process lobes directed ventrally, but diverge anteriorly. Long narrow sockets diverge at just over 90 degrees, bounded anteriorly by slender socket plates whose posterior half lies latero-posteriorly, and very close, to the cardinal process lobes. The socket is bounded posteriorly by a slight elevation of the hingeline. Very weak platform ends anteriorly in a broad, weak median ridge dividing the posterior pair of adductor muscle scars. The ridge bifurcates and then closes together again, leaving a faint pit (Pl. 14, fig. 5), after which it becomes narrow but more pronounced, dividing the anterior adductors and continuing, in some cases, nearly to the edge of the disc. No muscle bounding ridges near the umbo, but about a third of the way to the trail they suddenly appear, to persist strongly anteriorly for 5–10 mm., though never so pronounced as in the pedicle valve. Fairly large pseudopunctae visible everywhere except in the muscle field.

LECTOTYPE, here selected. GSM 11461, a pedicle valve from Wych Beds (Upper Llandovery), Gunwick Mill, Malvern Hills, Worcestershire.

DIMENSIONS (in cm.).

		l	w.
Bristol 12143	Pedicle valve	2·00	1·57
Bristol 12144	Pedicle valve	1·93	2·46
Bristol 12159	Pedicle valve	2·42	approx. 2·7
Bristol 12180	Pedicle valve	2·42	3·08
Bristol T.1	Pedicle valve	2·19	approx. 2·5
OUM C652	Tortworth pedicle valve . .	2·08	1·92
OUM C654	' May Hill sst.' pedicle valve .	2·59	approx. 2·7
OUM C5649	H-M-B pedicle valve . .	1·72	2·01
OUM C5641	H-M-B brachial valve length of trail . . .	1·16	approx. 1·1

The widths quoted are those of the hingeline, which is by no means always the widest part of the valve.

DISCUSSION. Lamont & Gilbert did not fully describe their varieties, but gave good illustrations of the pedicle valves (although no brachial valves were shown), and there is no doubt of the shells they had in mind, which are the same as that figured by Davidson (1871, pl. XLII, figs. 7, 8). The systematic situation surrounding this species and *Brachyprion arenacea* has been discussed elsewhere (Cocks 1967 : 257).

Lamont & Gilbert's two ' varieties ' are considered to be one homogeneous species, although this shows a remarkable range of variation in many details. They (1945) enumerated two differences between the varieties: (i) *lobatus* was more or less evenly curved, whereas *geniculatus* was geniculate, (ii) they had found no specimens of *lobatus* with concave muscle boundary ridges, although they admitted that convex forms were to be seen in both varieties. In fact a collection from Gunwick Mill shows all variations of geniculation in a single rock band, and a specimen from collection T-R-A, OUM C3690/1, shows a *lobatus* (*sensu* Lamont & Gilbert) shell shape with concave ridges.

Lamont & Gilbert (1945, p. 668) selected two syntypes, BU 397 and GSM 11461. As the first comes from 1030 feet down the Cooperative Society's borehole at Walsall, I propose to select the second specimen as lectotype. This is also the first specimen figured by Davidson (1871, pl. XLII, fig. 7) and comes from Gunwick Mill [Grid Ref. SO/7430 5152], a locality in which the species occurs up to 5 % and may be procured easily today. In addition the Birmingham specimen is poorly preserved and incomplete, whereas the lectotype is well preserved and shows the typical musculature.

The species is not common (never more than 5 %) at any locality, but has been found in the top part of the Upper Llandovery in beds of C_5 and C_6 age at Tortworth, May Hill, the Malverns, Ankerdine Hill, Shropshire, Rubery and Walsall, but has not so far been recovered outside the Welsh Borderland.

BELLIMURINA Cooper, 1956

Bellimurina sp.

(Pl. 14, figs. 9, 10)

A single specimen in the British Museum, B 8490, not accurately localized, but from 'Deerhope, Pentland Hills, Scotland,' may be referred to *Bellimurina*, a genus not so far recorded apart from Cooper's original description (1956) from the Middle Ordovician of America, and a record in the Caradocian of Girvan (Williams 1962). The specimen is a natural mould of an exterior of a brachial valve, and the attached cardinal area of a pedicle valve. Also on the same slab is a specimen of *Eoplectodonta* which confirms the late Llandovery age of the specimen. The ornament of the leptaeninid is typical of *Bellimurina*; differentiated parvicostellae, the larger of which separate the pattern of broken rugae. The shell is much larger (length 1·83 cm.) than contemporary *Cyphomenoidea*, which has a similar ornament, and the irregular shell shape and rough geniculation with the frilly lamellae on the gerontic trail have not been found in the latter subgenus.

Thus the stratigraphical range of *Bellimurina* is significantly increased.

III. ACKNOWLEDGMENTS

I would like to thank Mr. J. M. Edmonds and Mr. H. P. Powell of the Oxford University Museum (OUM) for the curation of the collections from Shropshire which I made whilst at Oxford and for access to those of Dr. A. M. Ziegler from the southern Welsh Borderland, with the latter's ready consent. Thanks also to Dr. A. W. A. Rushton of the Geological Survey & Museum (GSM), Mr. A. G. Brighton of the Sedgwick Museum, Cambridge (SM) and Dr. M. L. K. Curtis of the Bristol City Museum for the loan of other specimens. Most of the material is in the British Museum (Natural History) (B and BB).

I am grateful for valuable advice on aspects of the systematic work from Professor Alwyn Williams, and thank also Dr. W. S. McKerrow. I have had useful discussion with Dr. V. Havlíček, who in addition generously allowed me access to his recent (1968) monograph before its publication.

IV. REFERENCES

Amsden, T. W. 1949. Stratigraphy and paleontology of the Brownsport Formation (Silurian) of Western Tennessee. *Bull. Peabody Mus. Nat. Hist.*, New Haven, **5** : 1–138, pls. 1–34.

—— 1951. Brachiopods of the Henryhouse Formation (Silurian) of Oklahoma. *J. Paleont.* Tulsa, **25** : 69–96, pls. 15–20.

Bancroft, B. B. 1949. *Welsh Valentian Brachiopods and the* STROPHOMENA ANTIQUATA *group of fossil brachiopods.* 15 pp., 3 pls., privately printed. Mexborough.

Barrande, J. 1848. *Über die Brachiopoden der Silurischen Schichten von Boehmen.* part 2. 104 pp., pls. 16–23. Vienna.

—— 1879. *Système silurien du centre de la Bohême.* lère partie; volume V. Classe des Mollusques. Ordre des Brachiopodes. 226 pp., 153 pls. Prague & Paris.

Boucot, A. J., Johnson, J. G., Harper, C. W. & Walmsley, V. G. 1966. Silurian brachiopods and gastropods of Southern New Brunswick. *Bull. geol. Surv. Can.*, Ottawa, **140**: 1–145, pls. 1–18.

Chernychev, B. B. 1937. The Silurian brachiopods of Mongolia and Tuva (in Russian and English). *Trudy Mongolian Comm.*, **29**. *Izdatelstvo, Akad. sci. USSR.*, Moscow, 1–94, pls. 1–5.

Cocks, L. R. M. 1967. Llandovery stropheodontids from the Welsh Borderland. *Palaeontology*, London, **10** : 245–265, pls. 37–39.

—— 1967*a*. Depth patterns in Silurian marine communities. *Marine Geol.*, Amsterdam, **5**: 379–82.

Cooper, G. A. 1956. Chazyan and related brachiopods. *Smithson. Misc. Coll.*, Washington, **127** : 1–1245, pls. 1–269.

Dalman, J. W. 1828. Uppstallning och Beskrivning af de i sverige funne Terebratuliter. *K. Svenska Vetensk. Akad. Hand.*, Stockholm, for 1827 : 85–155, pls. 1–6.

Davidson, T. 1847. Observations on some of the Wenlock-limestone Brachiopoda, with descriptions of several new species. *Lond. geol. Jl.*, **1** : 52–65, pls. 12, 13.

— 1848. Mémoire sur les Brachiopodes du système silurien supérieur d'Angleterre. *Bull. Soc. géol. Fr.*, Paris, (2) **5** : 309–338, pl. 3.

—— 1868. On the Upper Silurian Brachiopoda of the Pentland Hills, and of Lesmahagow, in Lanarkshire. *Trans. geol. Soc. Glasgow* (Pal. Ser.) **1** : 1–24, pls. 1–3.

—— 1871. British fossil Brachiopoda, 3, Part 7, no. 4, Silurian. *Palaeontogr. Soc.* [*Monogr.*], London, **24** : 249–397, pls. 38–50.

—— 1883. Supplement to the fossil Brachiopoda, 5, Part 2, (Silurian). *Palaeontogr. Soc.* [*Monogr.*], London, **37** : 135–142, pls. 8–17.

FOERSTE, A. F. 1909. Preliminary notes on Cincinnatian fossils. *Bull. sci. labs Denison Univ.* **14** : 209–228, pl. 4.

GAGEL, C. 1890. Die Brachiopoden der Cambrischen und Silurischen Geschiebe im Diluvium der Provinzen Ost-und Westpreussen. *Beitr. Naturk. Preuss*, Konigsberg, **6** : 1–79, pls. 1–5.

HALL, J. & CLARKE, J. M. 1894. *An introduction to the study of the Genera of Palaeozoic Brachiopoda.* Part 2. Palaeontology of New York 8 : (xvi) 1–394, pls. 21–84. Albany.

HAVLÍČEK, V. 1963. Familie Leptaenidae (Brachiopoda) im Böhmischen Altpaläozoikum. *Cas. Národního Muz. Odd.*, Prague, **82** : 220–225, pls. 1, 2.

—— 1968. Brachiopoda of the suborder Strophomenida in Czechoslovakia. *Rozpr. Ústr. Úst. Geol.*, Praha, **33** : 1–225, pls. 1–52.

IMBRIE, J. 1956. Biometrical methods in the study of invertebrate fossils. *Bull. Am. Mus. nat. Hist.*, Washington, **108** : 211–246.

KINDLE, E. M. 1915. Notes on the geology and palaeontology of the Lower Saskatchewan River Valley. *Bull. geol. Surv. Can. Mus.*, Ottawa, **21** : 1–25, pls. 1–4.

LAMONT, A. 1947. Gala-Tarannon Beds in the Pentland Hills, near Edinburgh. *Geol. Mag., Lond.*, **84** : 193–208, 289–303.

—— & GILBERT, D. L. F. 1945. Upper Llandovery Brachiopoda from Coneygore Coppice and Old Storridge Common, near Alfrick, Worcestershire. *Ann. Mag. nat. Hist.*, London, ser. 11, **12** : 641–682, pls. 3–7.

LINDSTRÖM, G. 1860. Bidrag till kännedomen om Gotlands Brachiopoder. *Öfvers. K. Vetens. Akad. Förh.*, Stockholm, **17** : 337–382, pls. 12, 13.

MITCHELL, G. H. & MYKURA, W. 1962. The geology of the neighbourhood of Edinburgh. *Mem. geol. Surv. U.K.*, London, **32** : 1–159, pls. 1–4.

MURCHISON, R. I. 1839. *The Silurian system founded on geological researches in the counties of Salop, Hereford, Radnor, Montgomery, Caermarthen, Brecon, Pembroke, Monmouth, Gloucester, Worcester, and Stafford; with descriptions of the coal fields and overlying formations.* 768 pp., pls. 1–37. London.

NIKIFOROVA, O. I. & ANDREEVA, O. N. 1961. Stratigraphy of the Ordovician and Silurian of the Siberian Platform and its palaeontological basis. (Brachiopods). *Biostratigraphiya Palaeozoya Sibirskov Platformy*, Leningrad, **1** : 1–412, pls. 1–56.

REED, F. R. C. 1917. The Ordovician and Silurian Brachiopoda of the Girvan district. *Trans. roy. Soc. Edinb.*, **51** : 795–998, pls. 18–22.

SHALER, N. S. 1865. List of the Brachiopoda from the island of Anticosti sent by the Museum of Comparative Zoology to different institutions in exchange for other specimens, with annotations. *Bull. Mus. comp. Zool. Harv.*, Cambridge, **1** : 61–70.

SOKOLSKAYA, A. N. 1954. Strophomenids of the Russian Platform (in Russian). *Trudy palaeont. Inst.*, Moscow, **51** : 1–191, pls. 1–18.

—— 1960. Order Strophomenida. *In Osnovy Palaeontologii*; Mshanki, brakhiopody, vol. ed. T. G. SARYCHEVA, Moscow : 1–324, pls. 1–75.

SOWERBY, J. de C. 1823–25. *The Mineral Conchology of Great Britain*, **5** : 171 pp., pls. 408–503. London.

SPJELDNAES, N. 1957. The middle Ordovician of the Oslo Region, Norway. 8. Brachiopods of the Suborder Strophomenida. *Norsk geol. Tidsskr.*, Bergen, **37** : 1–214, pls. 1–14.

TWENHOFEL, W. H. 1928. Geology of Anticosti Island. *Mem. geol. Surv. Brch Can.*, Ottawa, **154** : 1–481, pls. 1–60.

VERNEUIL, P. E. P. de, 1848. Note sur quelques Brachiopodes de l'île de Gothland. *Bull. Soc. géol. Fr.*, Paris, (2) **5** : 339–353, pl. 4.

WAHLENBERG, G. 1821. Petrificata Telluris Svecanae examinata. *Nova Acta R. Soc. Scient. Upsal.*, **8** : 1–116, pls. 1–7 (for 1819).

WHITTARD, W. F. 1932. The stratigraphy of the Valentian rocks of Shropshire. The Longmynd-Shelve and Breidden outcrops. *Q. Jl geol. Soc. Lond.*, **87** : 859–902, pls. 58–62.

WILLIAMS, A. 1951. Llandovery brachiopods from Wales with special reference to the Llandovery district. *Q. Jl geol. Soc. Lond.*, **107** : 85–136, pls. 3–8.

—— 1953. The classification of the strophomenoid brachiopods. *J. Wash. Acad. Sci.*, **43** : 1–13.

—— 1953*a*. North American and European stropheodontids: their morphology and systematics. *Mem. geol. Soc. Am.*, New York, **56** : 1–67, pls. 1–12.

—— 1962. The stratigraphy and brachiopod faunas of the Barr and Lower Ardmillan Series (Caradoc) of the Girvan district of S.W. Ayrshire. *Mem. geol. Soc. Lond.*, **3** : 1–267, pls. 1–25.

—— 1963. The Caradocian brachiopod faunas of the Bala District, Merionethshire. *Bull. Br. Mus. nat. Hist.* (*Geol.*), London, **8**: 329–471, pls. 1–16.

—— *et al.* 1965. *Treatise on Invertebrate Paleontology, Part H, Brachiopoda.* Ed. R. C. Moore, Univ. Kansas and Geol. Soc. Am.: 1–297, figs. 1–746.

Ziegler, A. M. 1965. Silurian marine communities and their environmental significance. *Nature, London*, **207** : 270–272.

—— 1966. The Silurian brachiopod *Eocoelia hemisphaerica* (J. de C. Sowerby) and related species. *Palaeontology*, London, **9** : 523–543, pl. 83, 84.

——, Cocks, L. R. M. & Bambach, R. K. 1968. The Composition and Structure of Lower Silurian Marine Communities. *Lethaia*, Oslo, **1**: 1–27.

BRITISH MUSEUM 15 MAY 1966 NATURAL HISTORY

DESCRIPTIONS OF PLATES

Unless otherwise stated, all the specimens are coated with ammonium chloride. About half the photographs were taken by the author, the remainder by Mr. C. Keates. Specimens are in the British Museum (Natural History) (B and BB), Oxford University Museum (OUM), Sedgwick Museum, Cambridge (SMA) and Geological Survey and Museum (GSM)

PLATE 1

Pentlandina tartana Bancroft

Upper Llandovery, Bed D, Pentland Hills, Scotland. Collected by
Mr. Henderson, now in the Davidson Collection.

FIGS. 1, 2. BB 31447. Lectotype. Brachial internal mould and latex cast of it. ×2·0.

FIGS. 3, 4. BB 31448. Pedicle internal mould and latex cast of it. ×2·0.

FIGS. 5, 6. B 8485. Brachial internal mould and latex cast of it. Note pallial sinuses. ×2·0.

Pentlandina parva Bancroft

Upper Llandovery, The Frolic, Haverfordwest, Pembrokeshire.

FIG. 7. SMA 30013. Pedicle internal mould. ×1·9.

FIG. 8. SMA 30012. Holotype. Brachial internal mould. ×2·1.

Pentlandina parabola sp. nov.

Upper Llandovery, Purple Shale, Domas, Shropshire. Grid Ref. SJ/5936 0062.
Author's Collection.

FIG. 9. OUM C13507. Holotype. Partly exfoliated pedicle valve. ×3·0.

FIG. 10. OUM C13501. Complete specimen viewed posteriorly, although damaged at the apex and laterally. ×6·6.

FIG. 11. OUM C13512. Brachial internal mould. ×3·7.

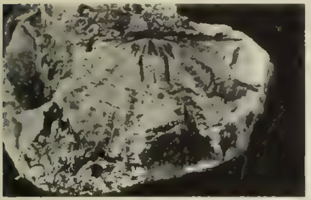
Upper Llandovery, Purple Shale, Boathouse Coppice, Shropshire.
Grid Ref. SJ/6205 0398. Author's Collection.

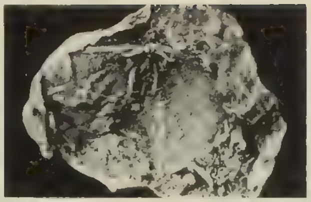
FIG. 12. OUM C12856. Pedicle internal mould. ×4·5.

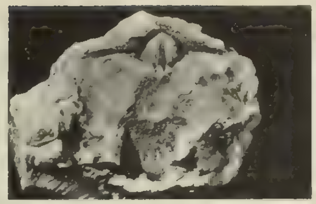
Pentlandina sp.

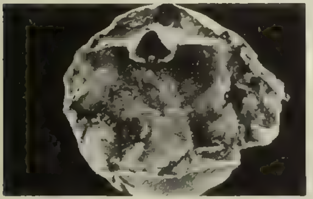
Middle Llandovery, Bog Quartzite, The Bog, Shropshire. Grid Ref.
SO/3510 9815. Author's Collection.

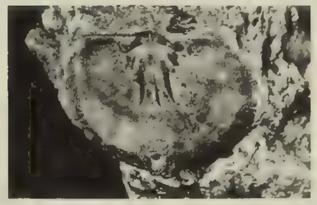
Fig. 13. BB 31299. Pedicle internal mould. ×2·0.

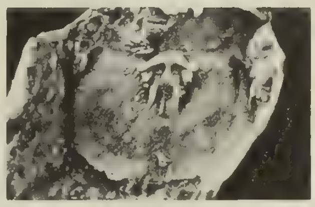

1

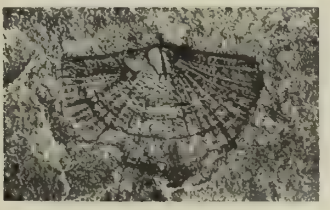

2

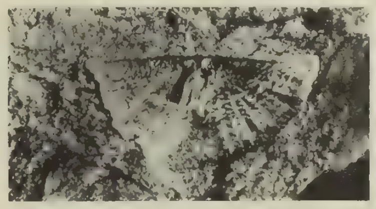

3

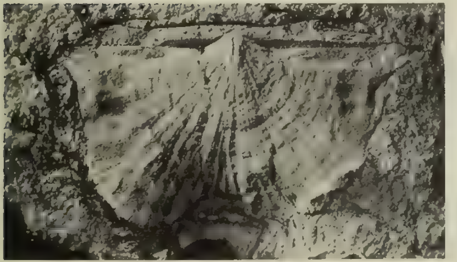

4

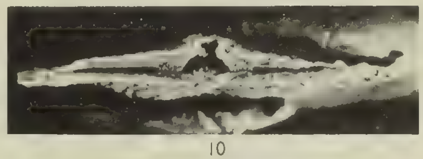

5

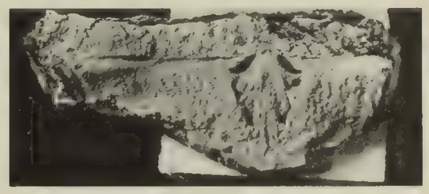

6

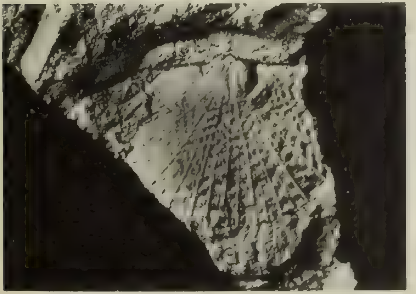

7


8


9


10


11


12

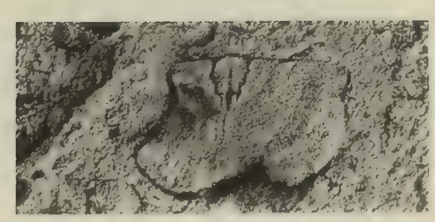

13

PLATE 2

Katastrophomena woodlandensis (Reed)

Middle Llandovery, Woodland Point, Girvan, Ayrshire. Gray Collection.

FIGS. 1, 2. B 54490. Lectotype. Internal view of pedicle valve and latex cast of it. ×1·5. Figured Reed 1917, pl. 18, fig. 21.

FIG. 3. B 73012. Paratype. Figured Reed 1917, pl. 19, fig. 4. External view of pedicle valve. ×1·5.

FIG. 4. B 54478. Paratype. Figured Reed 1917, pl. 19, fig. 3. Brachial internal mould. ×1·5.

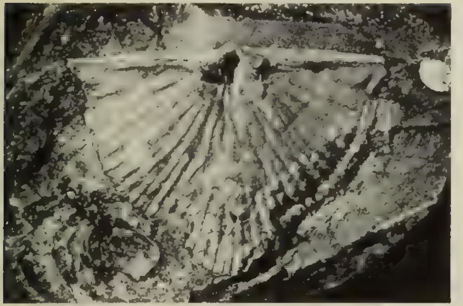
FIG. 5. BB 31452. Posterior view of two conjoined valves. ×1·5.

FIGS. 6, 7. BB 31426. Brachial internal mould, showing strong convexity and also pallial sinuses near the anterior margin. ×1·5.

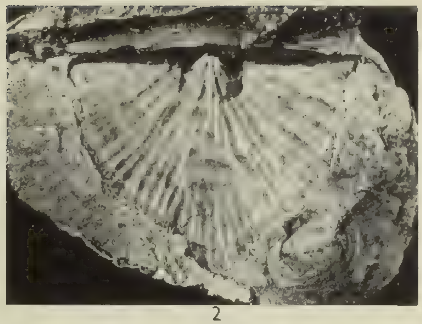
FIG. 8. BB 31420. Brachial internal mould which is nearly flat. ×1·5.

FIG. 9. BB 31425. Brachial internal mould. ×1·5.

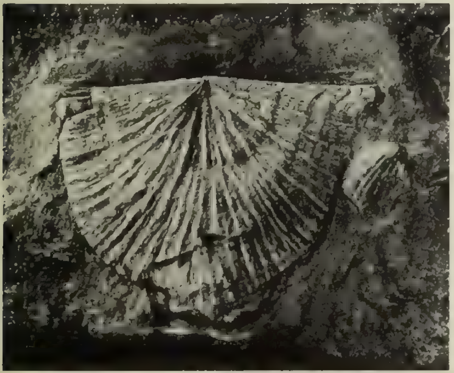
FIG. 10. BB 31427. Pedical internal mould. Note encrusting epizoon on inner surface. ×1·5.



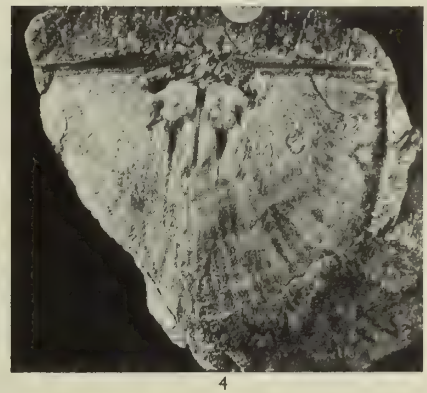
1



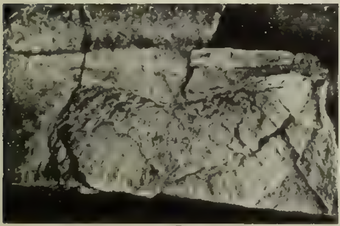
2



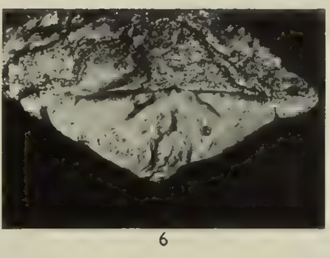
3



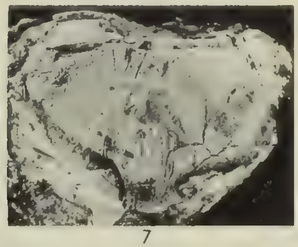
4



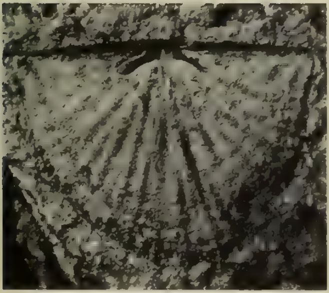
5



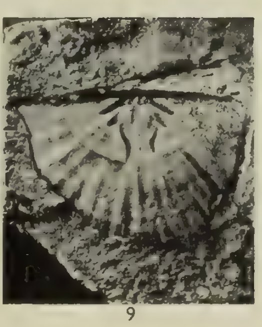
6



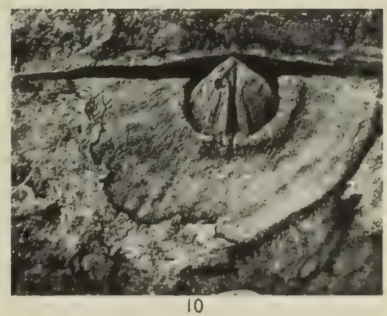
7



8



9



10

PLATE 3

Katastrophomena woodlandensis geniculata (Williams)

Upper Llandovery, C_1 beds, Sefin River, Llandovery, Carmarthenshire.
Grid Ref. SN/7418 2817.

FIG. 1. SMA 30008. Holotype. Pedicle internal mould. × 1·5.
FIG. 2. SMA 30007. Paratype. Brachial internal mould. × 1·5.

Katastrophomena scotica (Bancroft)

Lower Llandovery, Gasworks Mudstone, opposite entrance to gasworks,
Haverfordwest, Pembrokeshire. Grid Ref. SM/9588 1533.

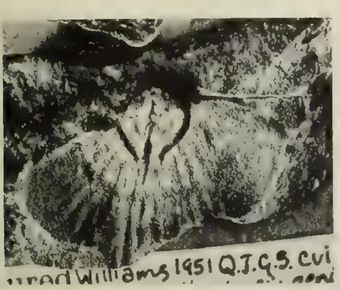
FIG. 3. SMA 32451. Brachial internal mould, figured Bancroft 1949, pl. 1, fig. 5. × 1·0.

FIGS. 4–7. SMA 32193. Internal mould, external mould, latex of internal mould and latex of external mould of pedicle valve. Paratype. Figured Bancroft 1949, pl. 1, figs. 6, 7. × 1.5. Turnbull Collection.

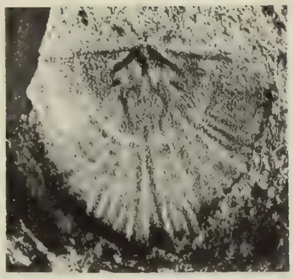
FIG. 8. SMA 32194. Lectotype. Pedicle internal mould, figured Bancroft 1949, pl. 1, fig. 4. × 1·5. Turnbull Collection.

Lower Llandovery, Gasworks Mudstone, quarry a few yards south of boathouse,
midway between the springs, The Frolic, Haverfordwest, Pembrokeshire.

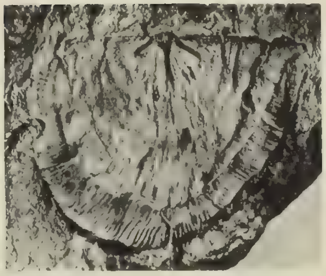
FIG. 9. SMA 30000. Pedicle internal moulds, the right hand one figured Williams 1951, pl. 7, fig. 2. × 1·5.


urad Williams 1951 Q.J.G.S. cvi

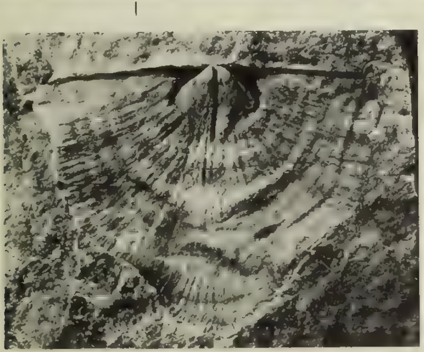
1



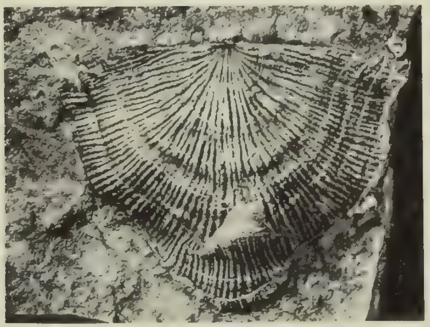
2



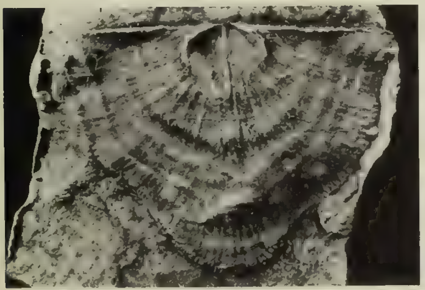
3



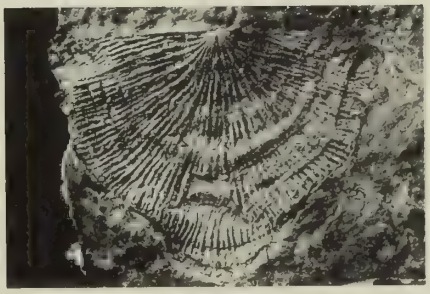
4



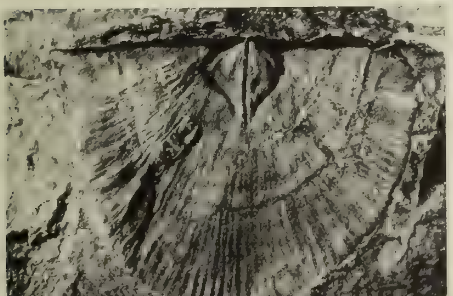
5



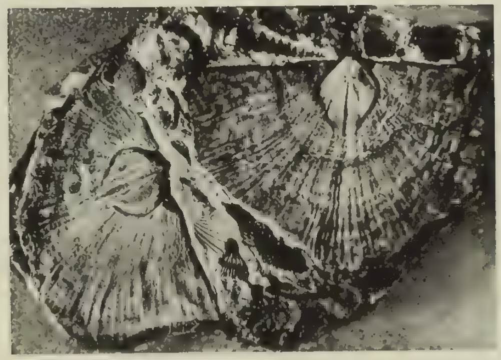
6



7



8



9

PLATE 4

Katastrophomena penkillensis (Reed)

Upper Llandovery, Bargany Pond Burn, Girvan Ayrshire. Gray Collection.

Fig. 1. B 73013. Lectotype. Brachial internal mould, figured Reed 1917, pl. 18, fig. 11. × 1·5.

Fig. 2. BB 31433. Pedicle internal mould. × 2·0.

Fig. 3. BB 31432. Brachial internal mould. × 2·0.

Fig. 4. B 54480. Brachial external mould, figured Reed 1917, pl. 18, fig. 13. × 1·5.

Fig. 5. B 73014. Pedicle internal mould, figured Reed 1917, pl. 18, fig. 12. × 2·0.

Upper Llandovery, Minsterley Formation, Minsterley-Habberley Lane, Shropshire. Grid Ref. SJ/3803 0487. Author's Collection.

Fig. 6. BB 31408. Pedicle internal mould. × 2·2.

Katastrophomena sp.

Middle Llandovery, Bog Quartzite, The Bog, Shropshire. Grid Ref. SO/3510 9815. Author's Collection.

Fig. 7. BB 31451. Brachial internal mould. × 3·0.

Upper Llandovery, Venusbank Formation, The Corners, near Betton, Shropshire, Grid Ref. SJ/3141 0252. Author's Collection.

Fig. 8. BB 31407. Pedicle internal mould. × 1·5.

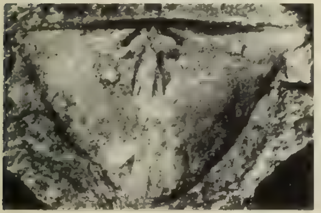
Leptaena martinensis sp. nov.

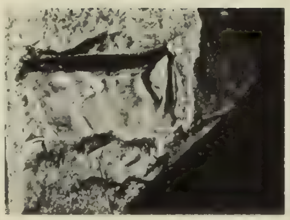
Lower Llandovery, Cartlett Mudstones, St. Martin's Cemetery, Haverfordwest, Pembrokeshire. Turnbull Collection.

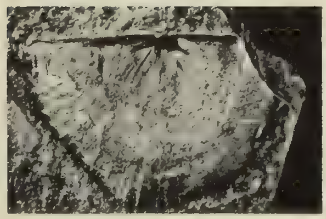
Figs. 9–11. SMA 31865. Internal mould, external mould, and latex cast of external mould of pedicle valve. Holotype. × 1·5.

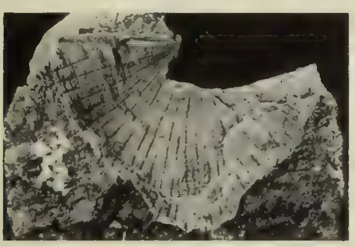
Fig. 12. SMA 31854. Brachial internal mould. × 1·5.

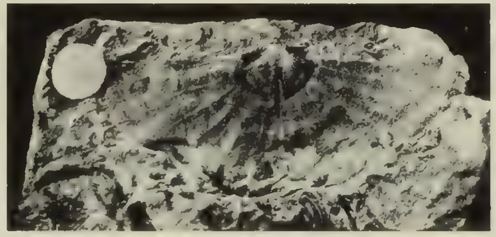
Fig. 13. SMA 31864. Internal mould of both valves, showing part of the brachial interior and part of the pedicle exterior. × 1·5.

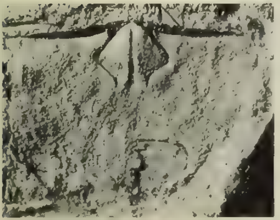

1

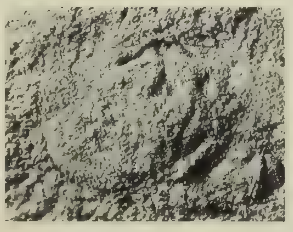

2

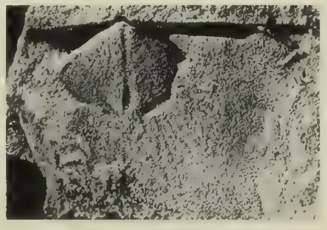

3

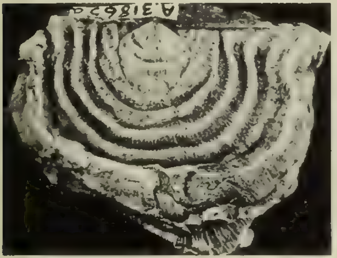

4

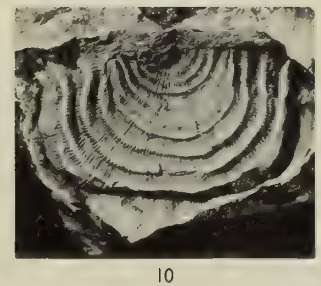

5

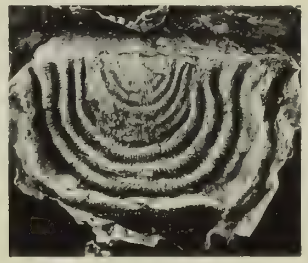

6

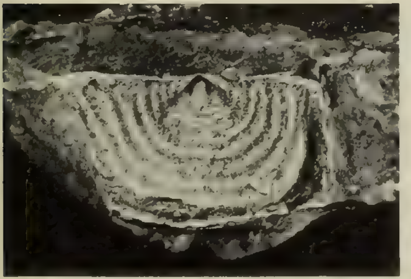

7


8


9


10


11


12

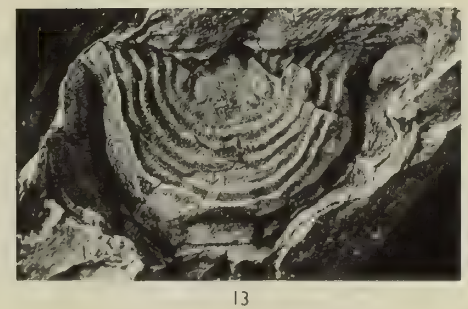

13

PLATE 5

Leptaena martinensis sp. nov.

Lower Llandovery, Cartlett Mudstones, St. Martin's Cemetery, Haverfordwest, Pembrokeshire. Turnbull Collection.

FIGS. 1–3. SMA 31859. Internal mould, external mould, and latex cast of external mould of pedicle valve of young individual. × 3·0.

Leptaena haverfordensis Bancroft

Lower Llandovery, Gasworks Mudstone, opposite entrance to gasworks, Haverfordwest, Pembrokeshire. Grid Ref. SM/9588 1533.

FIG. 4. SMA 32163. Lectotype. Pedicle internal mould figured by Bancroft, 1949, Pl. 1, fig. 20. × 1·5. Turnbull Collection.

FIG. 5. BB 31327. Pedicle internal mould. × 1·5. Author's Collection.

FIGS. 6–9. BB 31355. External mould, internal mould, latex of internal mould and latex of external mould of pedicle valve. × 1·5. C. P. Nuttall Collection.

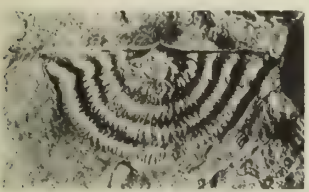
FIGS. 10, 13. BB 31359. Internal mould and latex of pedicle valve. × 1·5. C. P. Nuttall Collection.

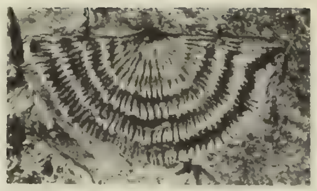
FIG. 11. SMA 32162. Pedicle internal mould figured Bancroft 1949, pl. 1, fig. 24. × 1·5.

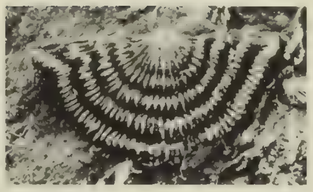
FIG. 12. BB 31363. Latex of brachial external mould. × 2·0. Author's Collection.

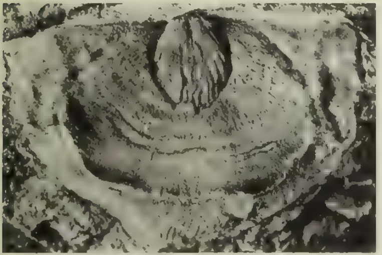
FIG. 14. SMA 40512. Pedicle internal mould, figured by Bancroft 1949, pl. 4, figs. 21, 22 [as *L. haverfordensis* var. *contracta*] × 1·6. Turnbull Collection.

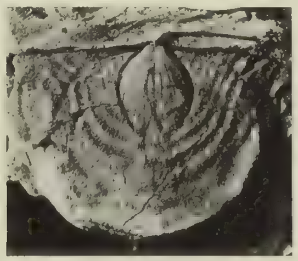
FIG. 15. SMA 32161. Brachial internal mould figured Bancroft 1949, pl. 1, fig. 23. × 1·5.

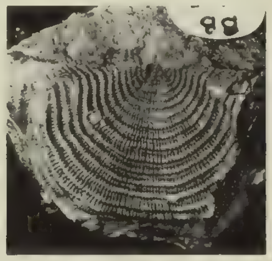

1

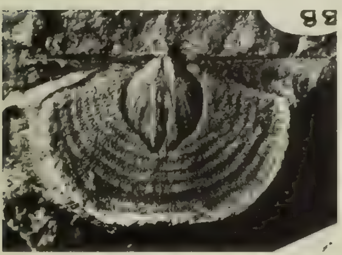

2

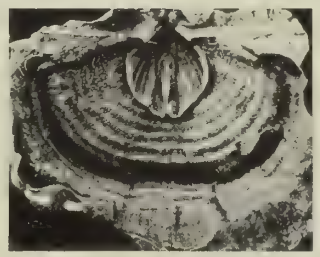

3

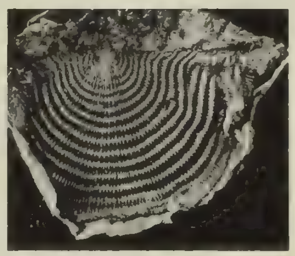

4

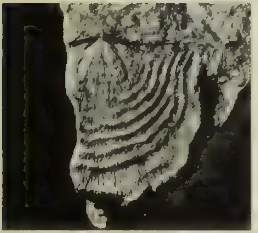

5

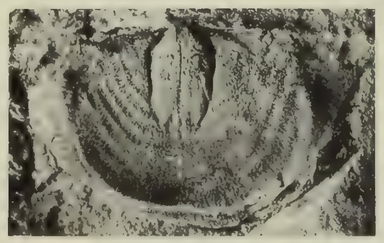

6

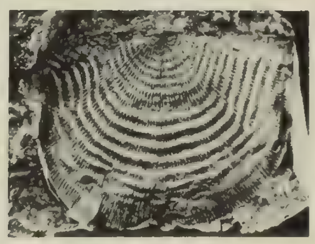

7

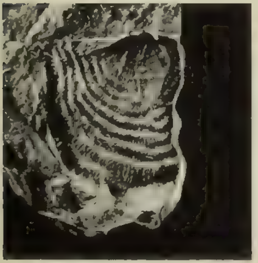

8

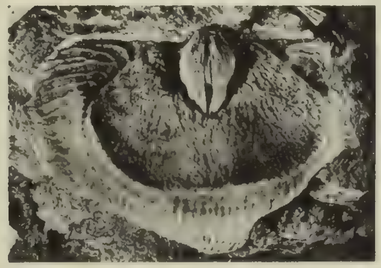

9


10


11


12


13


14

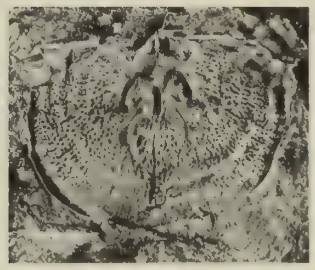

15

PLATE 6

Leptaena valida Bancroft

Upper Llandovery, C_1 beds, Sefin River, Llandovery, Carmarthenshire.
Grid Ref. SN/7418 2817. O. T. Jones Collection.

Figs. 1–3. SMA 35690. Holotype. Internal mould, external mould, and latex of external mould of pedicle valve. Figured Bancroft 1949, pl. 1, fig. 25. × 1·5.

Fig. 4. SMA 35691. Pedicle internal mould. Figured Bancroft 1949, pl. 1, fig. 26 [as *L. elongata*]. × 1·5.

Fig. 5. SMA 35692. Pedicle internal mould. Figured Bancroft 1949, pl. 1, fig. 27 [as *L. elongata*]. × 1·5.

Leptaena urbana Bancroft

Upper Llandovery, C_4 beds. O. T. Jones Collection 'Locality 27
NW/E λ8, quarry 500 yards NE of Cefn Cerig',
Llandovery, Carmarthenshire.

Fig. 6. SMA 35693. Lectotype. Pedicle internal mould. Figured Bancroft 1949, pl. 2, fig. 1. × 1·4.

Fig. 7. SMA 35694. Brachial internal mould. Figured Bancroft 1949, pl. 2, fig. 2. × 1·0.

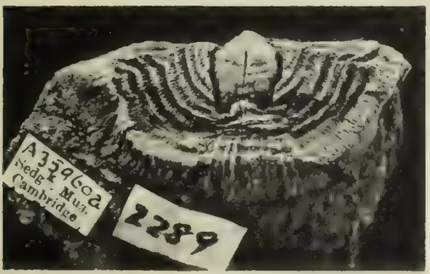
Leptaena contermina sp. nov.

Middle Llandovery, Venusbank Formation, Hope Quarry, Shropshire.
Grid Ref. SJ/3551 0208. Author's Collection.

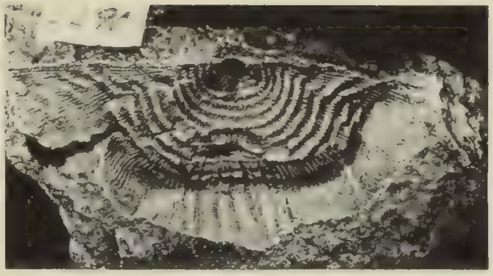
Figs. 8, 11. OUM C9168. Holotype. Pedicle internal mould and latex of it. × 2·0.

Figs. 9, 12. OUM C9147. Internal mould and latex of brachial valve. × 2·0.

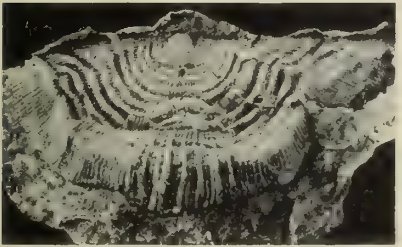
Figs. 10, 13. OUM C9155. Two views of brachial internal mould, the former oblique to show details of cardinalia.


A359602
Sedgk. Mus.
Cambridge
2289

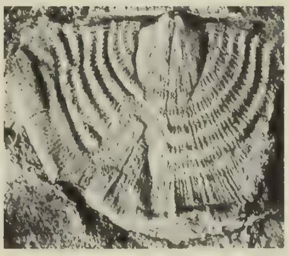
1



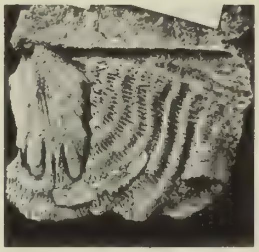
2



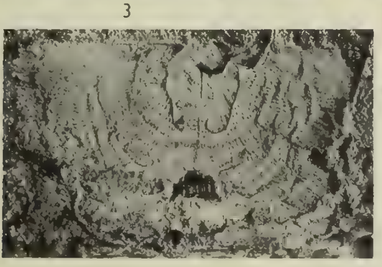
3



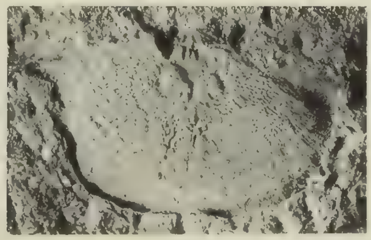
4



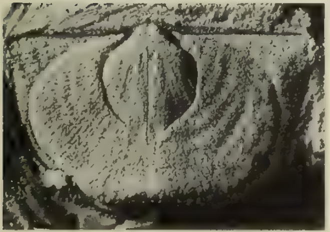
5



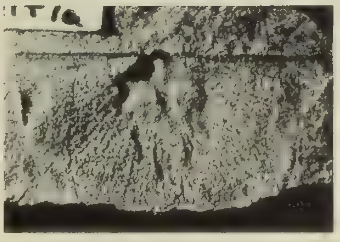
6



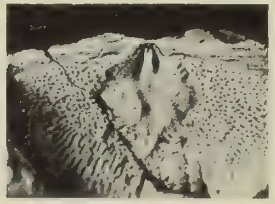
7



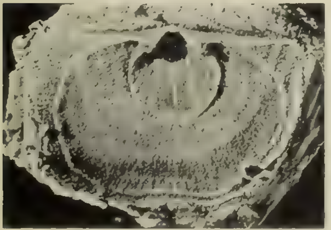
8



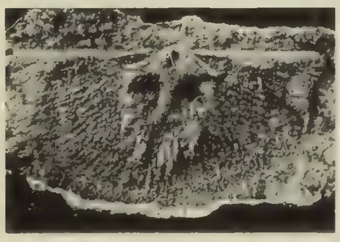
9



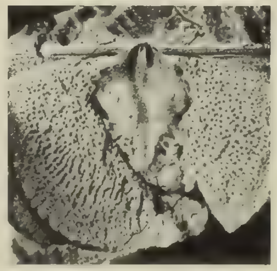
10



11



12



13

PLATE 7

Leptaena contermina sp. nov.

Middle Llandovery, Bog Quartzite, The Bog, Shropshire.
Grid Ref. SO/3510 9815. Author's Collection.

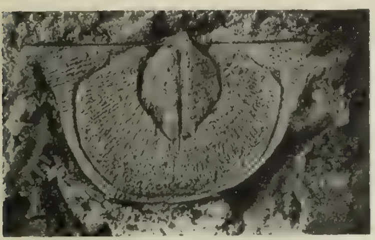
FIG. 1. BB 31280. Pedicle internal mould. ×1·5. Note also fragment of *Leonaspis* sp.
FIG. 2. BB 31289. Pedicle internal mould. ×2·0.
FIGS. 3, 4. OUM C10501. Brachial internal and external moulds. ×1·5.
FIG. 5. BB 31283. Brachial external mould. ×2·2.
FIG. 6. BB 31281. Pedicle internal mould. ×1·8.

Upper Llandovery, Yartleton Beds, May Hill, Gloucestershire.
Grid Ref. SO/6936 2271. A. M. Ziegler Collection.

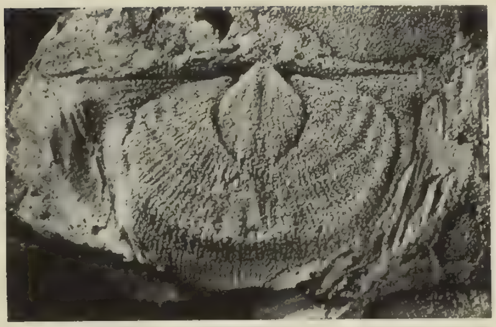
FIGS. 7, 8. OUM C2805. Brachial internal mould and latex cast of it. ×1·7.

Upper Llandovery, Cowleigh Park Beds, Ankerdine Hill, Worcestershire.
Grid Ref. SO/7376 5696. A. M. Ziegler Collection.

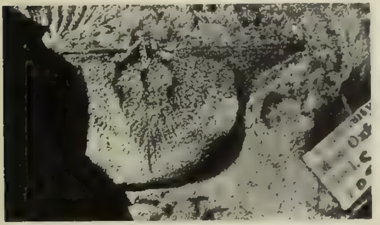
FIGS. 9–11. OUM C7390. Two views of pedicle internal mould and also a latex cast of it. ×2·0.



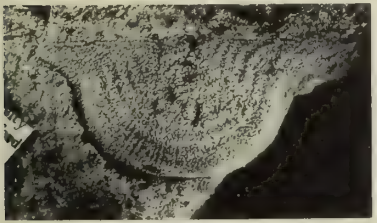
1



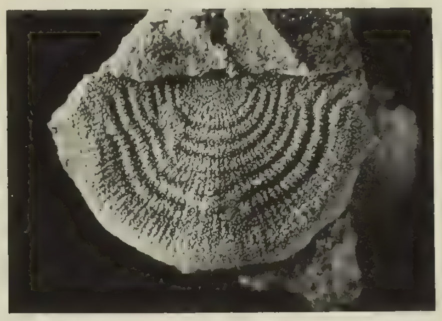
2



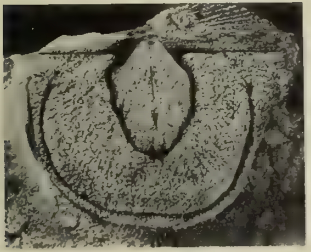
3



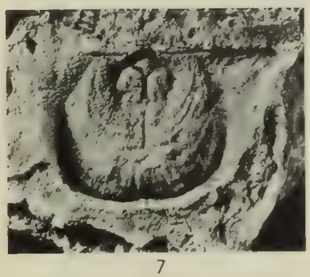
4



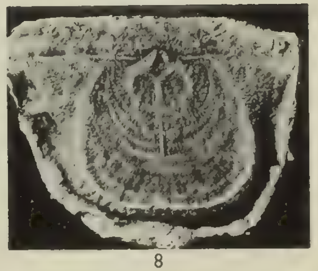
5



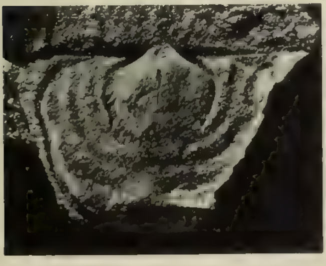
6



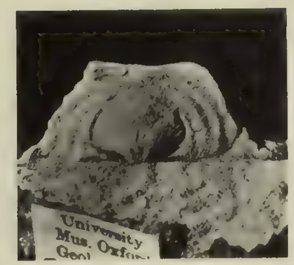
7



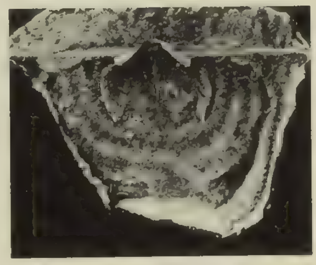
8



9


University
Mus. Oxford
Geol

10



11

PLATE 8

Leptaena valentia sp. nov.

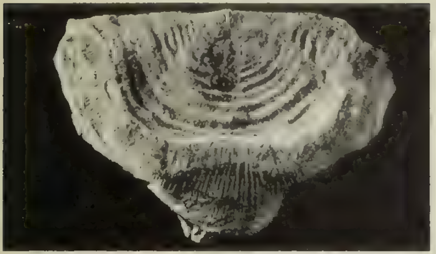
Middle Llandovery, Woodland Point, Girvan, Ayrshire, Scotland.
Gray Collection.

FIGS. 1–3. B 73340. Holotype. Complete shell, figured Reed 1917, pl. 13, fig. 5. × 1·5.
FIGS. 4, 5. BB 55620. Latex cast and internal mould of pedicle valve. × 1·5.
FIG. 6. BB 55718. Latex cast of brachial external. × 2·0.
FIGS. 7, 8. BB 55688. Latex cast (× 1·6) and internal (× 2·0) of brachial valve.

Leptaena valentia mullochensis subsp. nov.

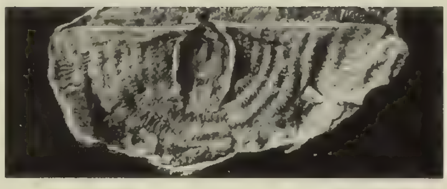
Lower Llandovery, Mulloch Hill, Girvan, Ayrshire, Scotland.
Gray Collection.

FIG. 9. B 73384. Holotype. Partly exfoliated pedicle valve, figured Reed 1917, pl 13, fig. 4. × 1·5.
FIGS. 10, 11. B 73379. Internal mould of both valves viewed from either side. × 2·0.
FIG. 12. BB 31375. Pedicle internal mould. × 2·0.
FIG. 13. BB 31383. Pedicle internal mould. × 2·0.
FIG. 14. B 73381. Pedicle internal mould. × 2·0.
FIG. 15. BB 31386. Brachial internal mould. × 2·0.

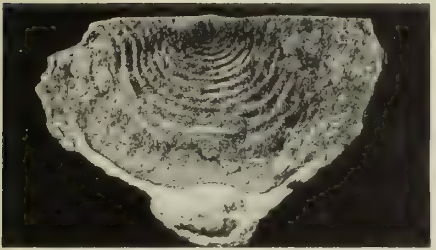


1

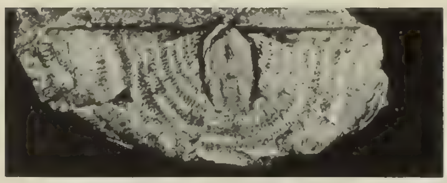
3



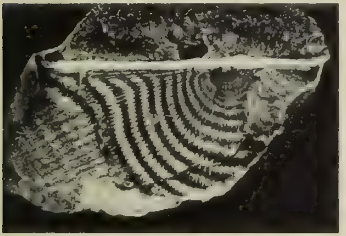
4



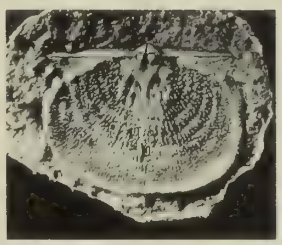
2



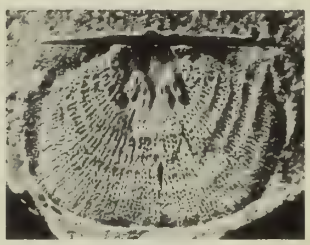
5



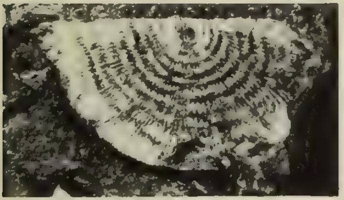
6



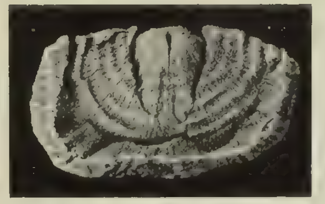
7



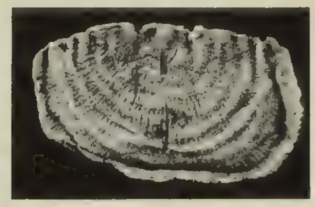
8



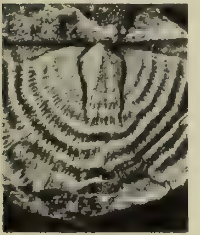
9



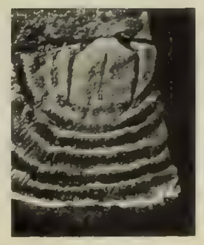
10



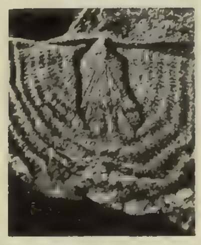
11



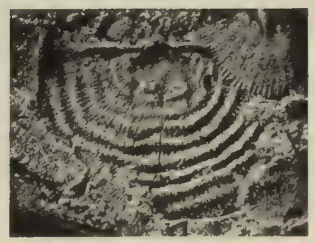
12



13



14



15

PLATE 9

Leptaena zeta Lamont, 1947

Upper Llandovery, Penkill, Girvan, Ayrshire, Scotland.
Gray Collection.

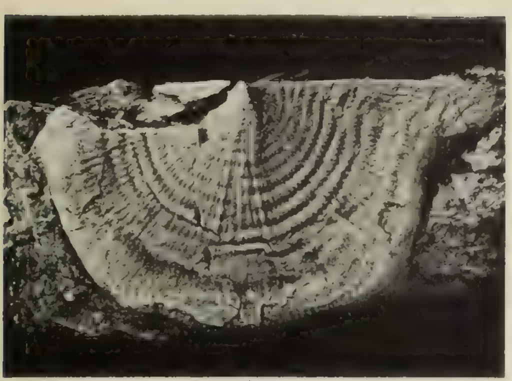
FIG. 1. B 73355. Lectotype. Pedicle valve, figured Reed 1917, pl. 13, fig. 8. × 1·5.
FIG. 2. BB 31302. Pedicle internal mould. × 1·8.
FIG. 3. BB 31305. Pedicle internal mould. × 1·8.
FIG. 4. BB 31303. Pedicle internal mould. × 1·8.

Upper Llandovery, Bargany Pond Burn, Girvan, Ayrshire, Scotland

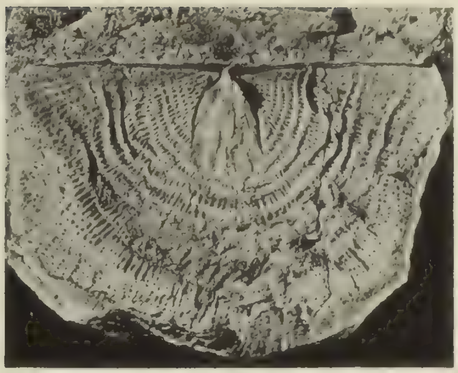
FIG. 5. GSM 4108. Brachial internal mould. × 1·8.

Upper Llandovery, Minsterley Formation, Minsterley-Habberley Lane, Shropshire.
Grid Ref. SJ/3803 0487. Author's Collection.

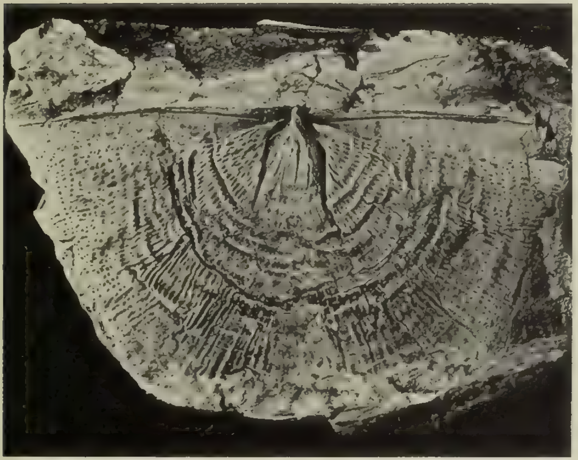
FIG. 6. BB 31468. Brachial internal mould. × 2·2.



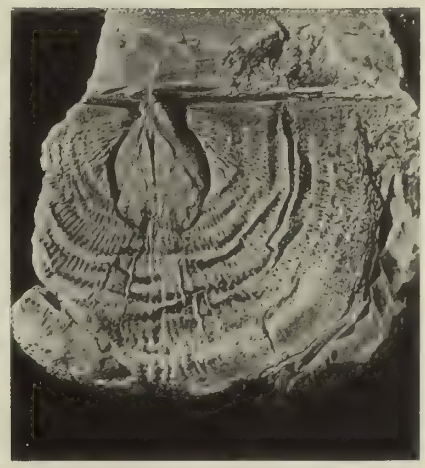
1



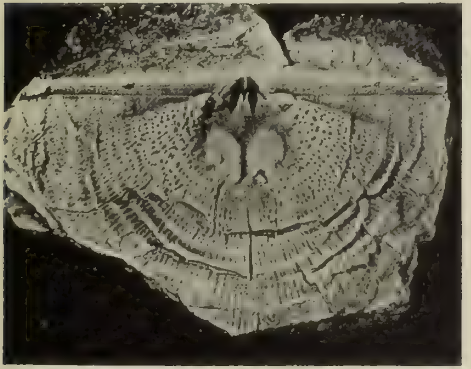
2



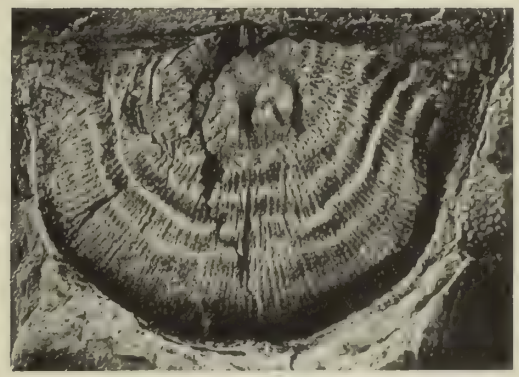
3



4



5



6

PLATE 10

Leptaena reedi sp. nov.

Middle Llandovery, Woodland Point, Girvan, Ayrshire.
Gray Collection.

FIG. 1. B 73341. Complete shell, figured Reed 1917, pl. 13, fig. 7. Holotype. × 3·0.

FIGS. 2, 3. B 73345. Pedicle valve. × 3·0.

FIGS. 4, 5. BB 31460. External mould of brachial valve and pedicle interarea, and latex cast of them. × 2·0.

FIG. 6. BB 31459. Brachial internal. × 3·0.

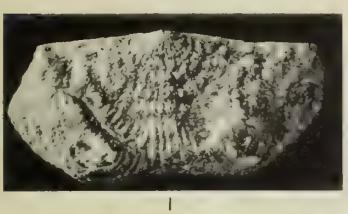
FIG. 7. BB 31458. Pedicle internal mould. × 3·0.

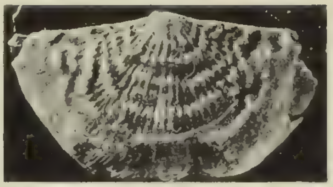
FIG. 8. B 73342. Brachial internal. × 2·0.

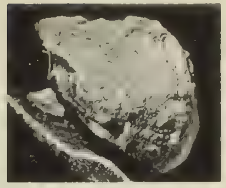
FIGS. 9–12. BB 31457. Two views each of pedicle internal mould and latex cast of it. Note close association with *L. valentia*. × 2·0.

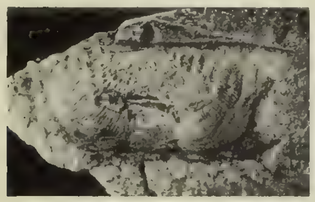
FIG. 13. BB 31461. Brachial external mould. × 3·0.

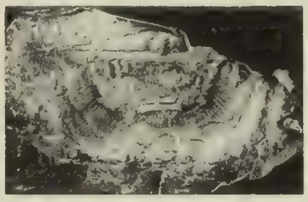
FIG. 14. B 73346. Complete shell. × 3·0.

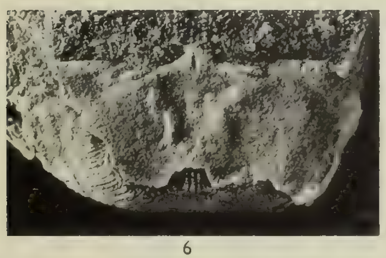

1

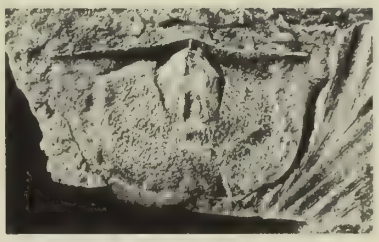

2

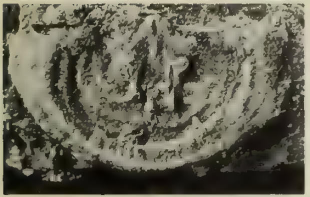

3

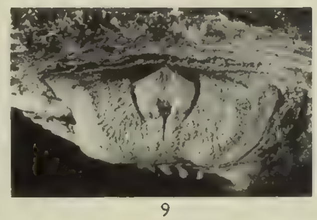

4

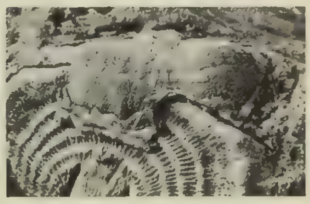

5

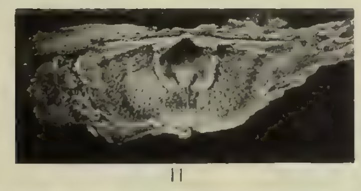

6

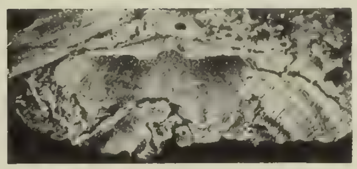

7

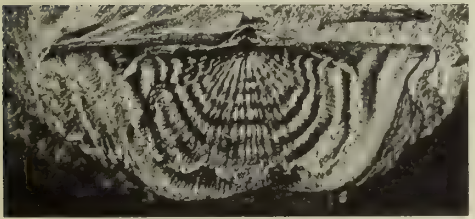

8


9


10


11


12


13

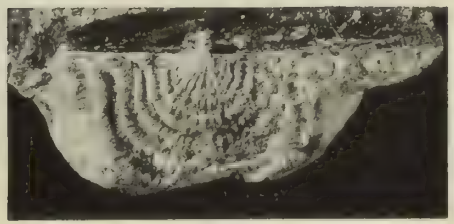

14

PLATE 11

Leptaena ziegleri sp. nov.

Upper Llandovery, Wych Beds, Malvern Hills, Herefordshire.
Grid Ref. SO/7612 3811. A. M. Ziegler Collection.

FIGS. 1, 2. OUM C4146. Pedicle internal mould and latex of it. Holotype. × 3·3.

FIGS. 3–5. OUM C4136. Internal mould, latex of it and external mould of brachial valve. × 3·3.

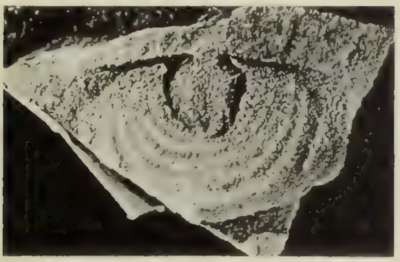
Leptaena quadrata Bancroft

Upper Llandovery. O. T. Jones locality 'Loc. K, below path SW of Uzmaston',
The Frolic, near Haverfordwest, Pembrokeshire.

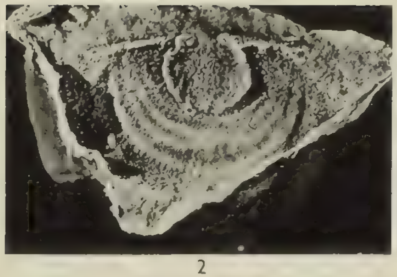
FIGS. 6–8. SMA 32437. Internal mould, external mould, and latex of external mould of pedicle valve. Lectotype. Figured Bancroft 1949 pl. 1, fig. 28. × 3·0.

FIG. 9. SMA 32438. Brachial internal mould, figured Bancroft 1949, pl. 1, fig. 29. × 3·0.

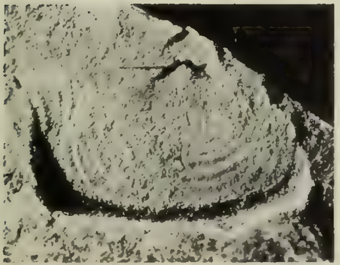
FIG. 10. SMA 32439. Pedicle internal mould, figured Bancroft 1949, pl. 1, fig. 30. × 3·5.



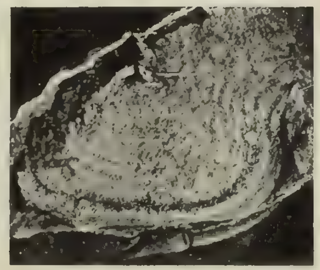
1



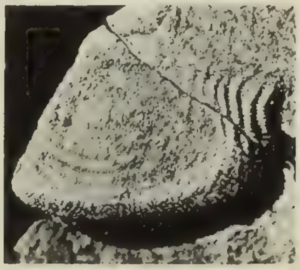
2



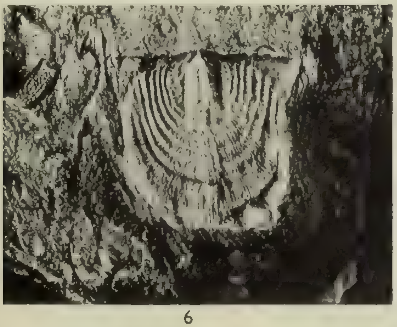
3



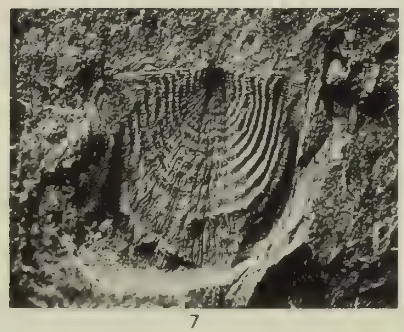
4



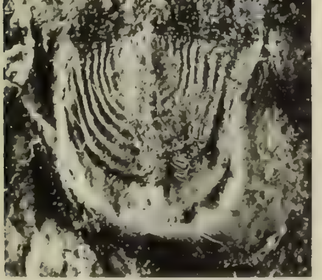
5



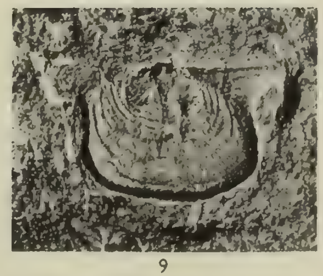
6



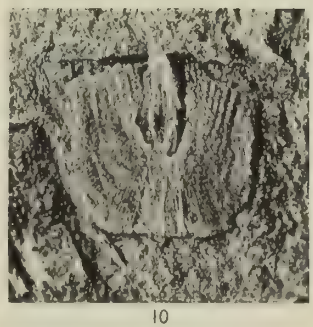
7



8



9



10

PLATE 12

Leptaena purpurea sp. nov.

Upper Llandovery, Purple Shale, Shropshire, various localities.
Collected W. F. Whittard and author.

FIG. 1. BB 31465. Holotype. Pedicle internal mould, also pedicle internal mould of *Glassia obovata* (J. de C. Sowerby). Domas. Grid Ref. SJ/5936 0062. × 2·5.

FIG. 2. BB 31463. Pedicle internal mould. Gippols Dingle. Grid Ref. SO/5727 9937. × 2·5.

FIG. 3. BB 31466. Brachial valve, also *Aegiria grayi* (Davidson). Hughley. Grid Ref. SO/5639 9809. × 3·0.

FIG. 4. OUM C12062. Pedicle internal mould. Onny River. Grid Ref. S/O4260 8532. × 3·0.

FIG. 5. BB 31464. Pedicle internal mould. Hughley. Grid Ref. SO/5637 9795. × 2·5.

Leptaena cf. ***purpurea*** sp. nov.

Upper Llandovery, Damery Beds, eastern bank of railway cutting, immediately north of road bridge, Charfield Station, Gloucestershire.
M. L. K. Curtis Collection.

FIG. 6. Bristol University Museum 12101. Pedicle internal mould. × 1·8.

Leptaena sp.

Upper Llandovery, Purple Shale, ' Harley ', Shropshire.
W. F. Whittard Collection.

FIGS. 7, 8. BB 31467. Complete shell viewed dorsally (× 1·6) and posteriorly (× 2·5).

Cyphomena (Cyphomenoidea) wisgoriensis (Lamont & Gilbert, 1945)

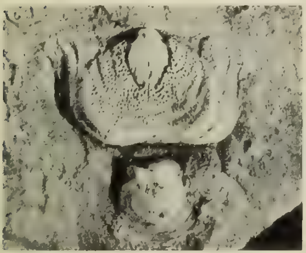
Upper Llandovery, Wyche Beds, Malvern Hills, Herefordshire.
Grid Ref. SO/7430 5152. A. M. Ziegler Collection.

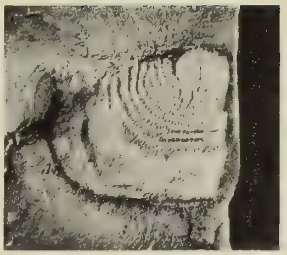
FIG. 9. OUM C5638. Pedicle internal mould. × 1·7.
FIG. 10. OUM C5631. Brachial internal mould. × 1·9.
FIG. 11. OUM C5615. Brachial internal mould. × 2·0.
FIG. 12. OUM C5612. Brachial external mould. × 2·8.

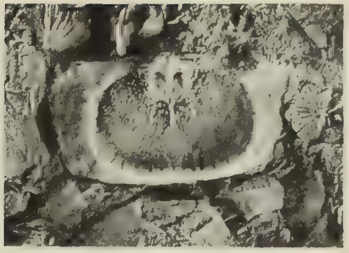
Cyphomena (Laevicyphomena) feliciter sp. nov.

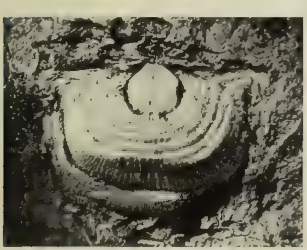
Middle Llandovery, Bog Quartzite, The Bog, Shropshire.
Grid Ref. SO/3510 9815. Author's Collection.

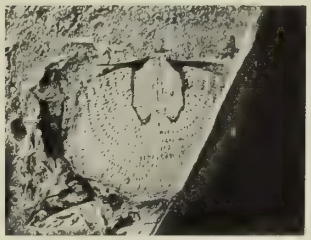
FIGS. 13, 14. BB 31346. Holotype. Pedicle internal mould and latex cast of it. × 3·0.

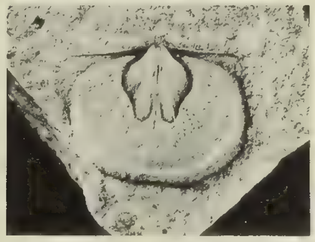

1

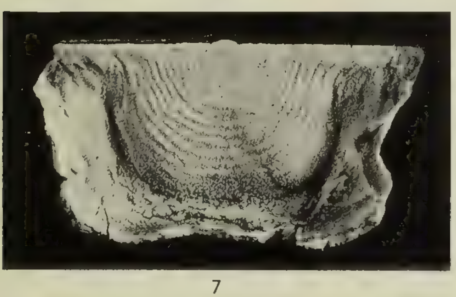

2

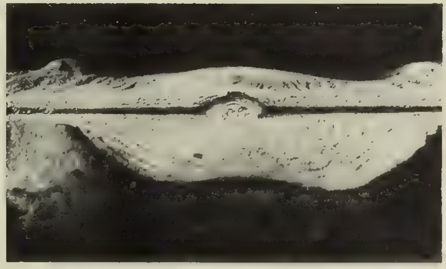

3

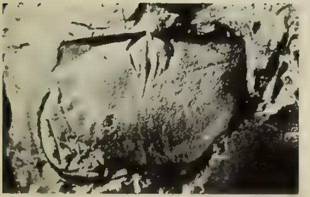

4

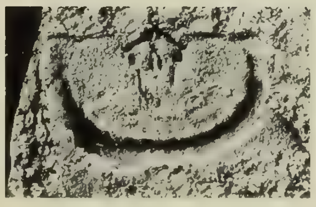

5

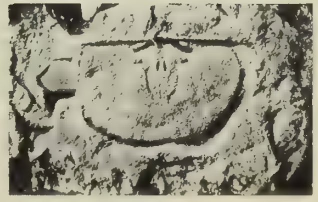

6

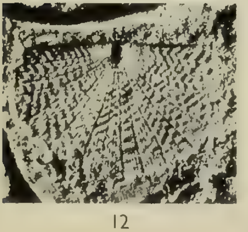

7

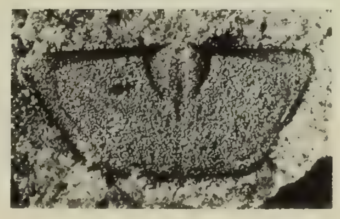

8


9


10


11


12


13

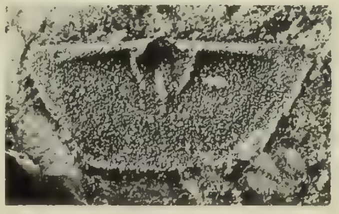

14

PLATE 13

Cyphomena (Laevicyphomena) feliciter sp. nov.

Middle Llandovery, Bog Quartzite, The Bog, Shropshire.
Grid Ref. SO/3510 9815. Author's Collection.

FIG. 1. OUM C9895. Pedicle internal mould. ×2·3.
FIG. 2. BB 31347. Brachial internal mould. ×2·7.
FIG. 3. BB 31351. Brachial internal mould. ×2·6.
FIG. 4. BB 31348. Brachial internal mould. ×2·0.
FIGS. 5, 6. OUM C9893. Brachial internal and external moulds. ×2·5.

Middle Llandovery, Venusbank Formation, Josey's Wood, Shropshire.
Grid Ref. SJ/3653 0221. Author's Collection.

FIG. 7. OUM C10988. Pedicle internal mould. ×2·2.

Middle Llandovery, Bog Quartzite, Napp Outlier, Shropshire.
Grid Ref. SO/3491 9932. W. F. Whittard Collection.

FIGS. 8, 9. BB 31352. Pedicle internal mould (×2·0) and latex cast of it (×3·0).

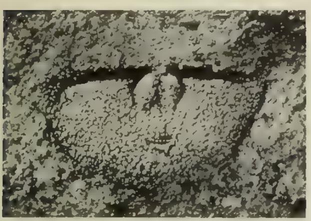
Mackerrovia lobatus (Lamont & Gilbert, 1945)

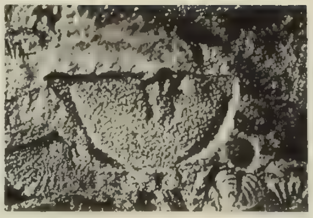
Upper Llandovery, Damery Beds, old working about 260 yards W 25° N of
Damery Bridge, near Tortworth, Gloucestershire.
M. L. K. Curtis Collection.

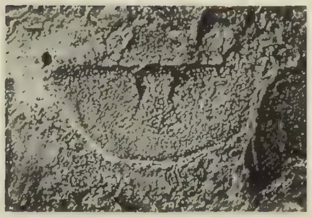
FIGS. 10–12. Bristol University Museum 12180. Pedicle internal mould and latex cast of it. ×1·5.

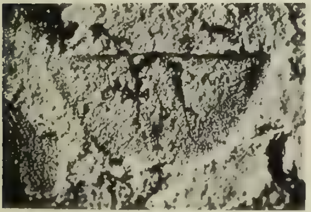
Upper Llandovery, Damery Beds, Ironmill Grove, Damery, near Tortworth,
Gloucestershire. M. L. K. Curtis Collection.

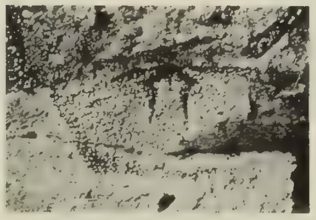
FIGS. 13–15. Bristol University Museum 12143. Internal mould, latex cast and external mould of pedicle valve. ×1·5.

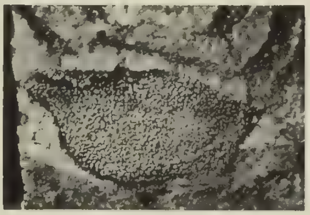

1

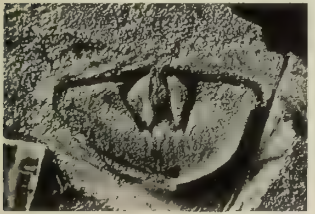

2

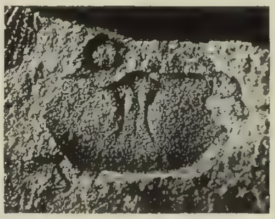

3

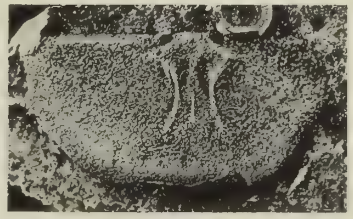

4

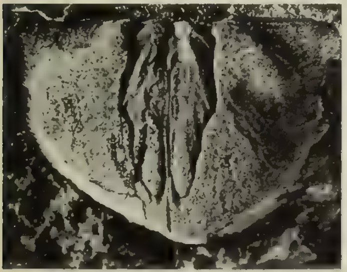

5

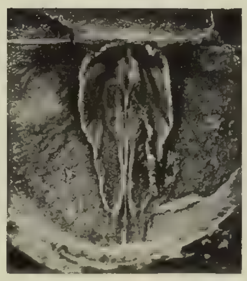

6

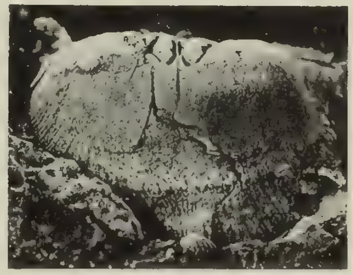

7

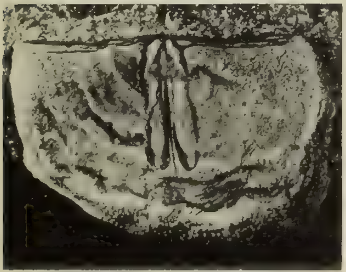

8

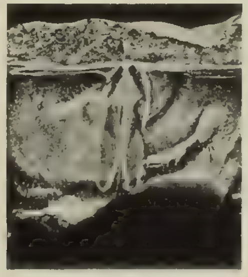

9


10


11


12


13


14

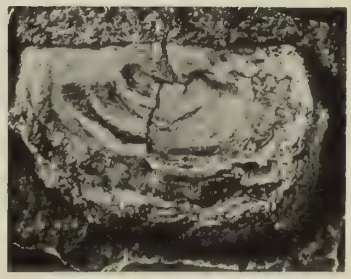

15

PLATE 14

Mackerrovia lobatus (Lamont & Gilbert, 1945)

Upper Llandovery, Damery Beds, Tortworth Inlier, various localities.
M. L. K. Curtis and A. M. Ziegler Collections.

FIGS. 1, 2. Bristol University Museum 12159. Avening Green. Pedicle internal mould and latex cast of it. × 1·5.

FIG. 3. Bristol City Museum Tl. Western end of Ironmill Wood, Damery. Pedicle internal mould. × 1·7.

FIG. 4. Bristol University Museum 12144. Field, 200 yards NW of Avening Green. Pedicle internal mould. × 1·4.

FIG. 5. OUM C3686. Railway cutting 60 yards NW of railway bridge at Charfield Station. Brachial internal mould. × 2·0.

Upper Llandovery, Wych Beds, Malvern Hills, Herefordshire.
Grid Ref. SO/7430 5152. A. M. Ziegler Collection.

FIG. 6. OUM C5649. Pedicle internal mould. × 2·0.

FIG. 8. OUM C5641. Brachial internal mould. × 2·0.

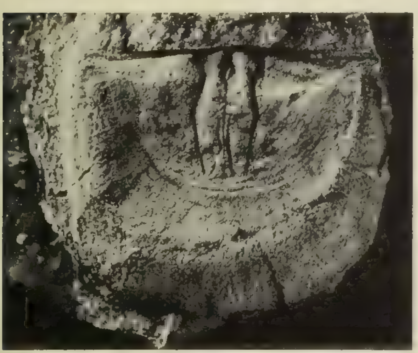
Upper Llandovery, in Oxford University Museum with old label 'May Hill Sandstone' only. The lithology is probably that of the May Hill Inlier, Gloucestershire.

FIG. 7. OUM C654. Pedicle and brachial internal moulds. × 1·2.

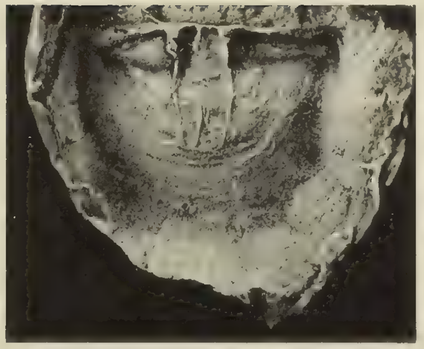
Bellimurina sp.

Upper Llandovery, Deerhope Burn, Pentland Hills, Scotland.

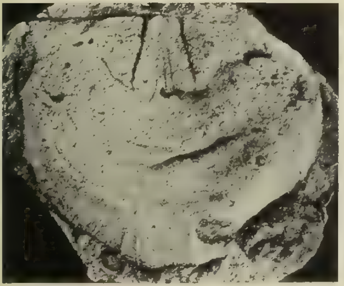
FIGS. 9, 10. B 8490. External mould and latex cast of brachial external and pedicle interarea. × 1·5.



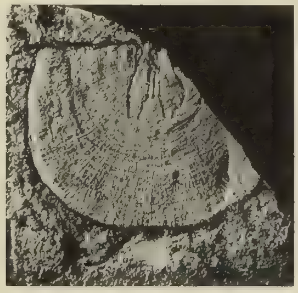
1



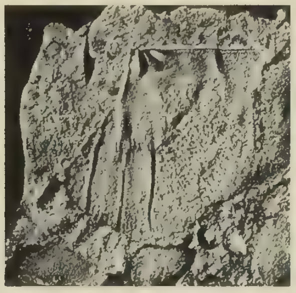
2



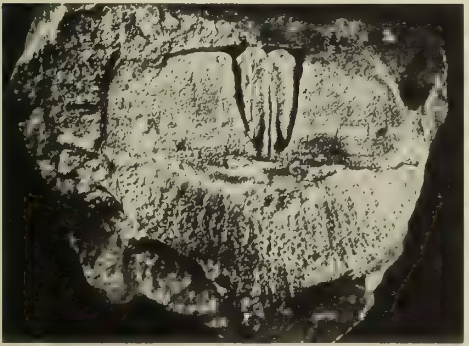
3



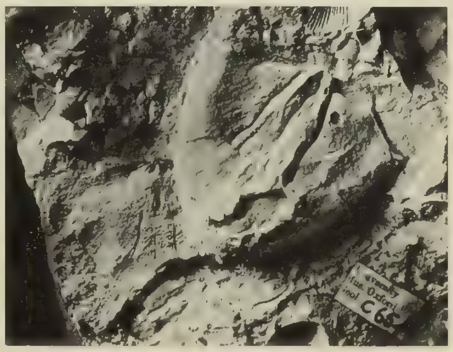
4



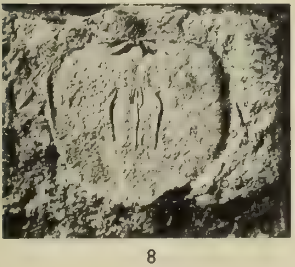
5



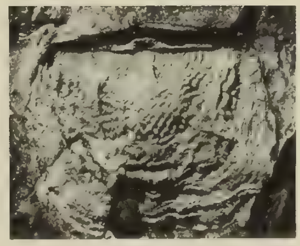
6


Mus. Oxford
C 66

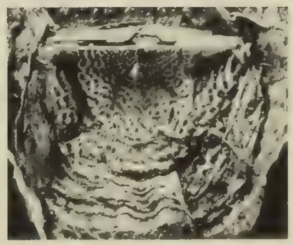
7



8



9



10

INDEX TO VOLUME XV

New taxonomic names and the page numbers of the principal references are printed in **Bold** type. An asterisk (*) denotes a figure.

acanthophyllids 206
Acanthophyllinae 206
Acanthophyllum 188
Acervularia 211–13, 231
  baltica 212
  coronata 213–15, 220
  goldfussi 231, 236, 247–9, 253
  limitata 248–9, 253
  macrommata 213
  pentagona 233, 248
  roemeri 212, 214–5, 220
  seriaca 253, 257
  troscheli 228
? *Acervularia roemeri* var. *β concinna* 243, 245
Acinophyllum 271–73
  simcoense 272
Actinocyathus 212
  hennahii 214
'algae' 136, 151, 161
Aegiromena 88–92
Allovirgatites 5, **22**
  robustus 45–6
  tutcheri 48–9
  versicostatus 45–6
  woodwardi 22, 45–6
Alveolites 188
Ammonites 1–79
  Evolution 64–66
  Homeomorphy 19–20, 23, 66, 75
  Intersex 54
  Kimmeridgian faunas 4–5, 66–76
  Rib characters 22–3, 25, 32, 38, 40, 51
  Sexual Dimorphism 15–18
Ammonites biplex 5
  gigas 12
  gravesianus 12, 14
  pectinatus 14, 19, 59
  scruposus 19
  ulmensis 19
  virgatus 18
Ammonoidea see Cephalopoda
Amphistrophia 319
  whittardi 313
Ampyx 93–4
  abnormalis 95
  camurus 94
  linleyensis 94
  nasutus 94
  nitidus 86, 88, **93**, 94–95 ; Pl. 5, figs. 5, 8–11
  virginiensis 94
Anomites rhomboidalis 300
Arachnophyllum 211
  hennahi 214
Arkellites 8, 9, 18, 21, **24**, 25, 64, 65*
Asaphidae 121
Asaphid gen. & sp. indet. 91, **121**, 122 ; Pl. 10, figs. 2, 5
Aschemonia 132
  gigantea 134
Astraea hennahii 212, 214
  intercellulosa 214, 215, 220
  pentagona 233
'*Astrea hennahii*' 184, 212, 214–15
  parallela 212
Astrea (*Favastrea*) *pentagona* 233, 247, 253
Astrea (*Siderastrea*) *hennahi* 214
Ataxioceras 23
ataxioceratids 24
Aulacostephanus 68
Aulina 212

Barton Quarry, Devon (Middle Devonian) 186–187, **188**, 201
  samples 217, 218, 220, 225
Bedinan Formation, Turkey **85**, 86*, 87*, 88, 89, 91, 97
  faunas, age of 91
    relationship 91
Bellimurina 299, 321
Bellimurina sp. **321** ; Pl. 14, figs. 9, 10
Bensonastraea 214
Billingsastraea 206, 207, 213, 231, 232
  ? *battersbyi* 186
  goldfussi 248
  verneuili 232
Bilobites 153
Borings, trace fossils 156, 161
Brachiopoda 283–324
  homeomorphy 319
  lineages 286, 299, 302*, 315
  phylogeny 286, 299, 302*, 315
  stratigraphical
    Great Britain
      Upper Ordovician 294, 299, 300, 315

    Silurian (283–324), 286, 294, 299, 300, 315
      Landovery 286, 288, 291–294, 298–301, 302*
    Kimmeridgian 10
  Turkey, Ordovician 88, 90, 92
Brachyprion 319
  arenacea 321
  arenaceus var. *lobatus* 319, 321
    var. *geniculatus* 319, 321
Bracteoleptaena 299
Brongniartella 92, 118–120
  bisulcata 119
  caradocia 119
  inexpectata 119, 120
  levis 88, **118**, 119, 120 ; Pl. 8, figs. 2, 3, 6
  platynota 92, 119
  sp. 88 ; Pl. 8, figs. 1, 5
Burrows, Trace fossils. See also *Thalassinoides*, *Chondrites*, *Spongeliomorpha* and '*Terebrella*'.
  Association with hardgrounds 147–8
    laminated structures 133, 138–41
  burrowing organisms 137, 138, 147–161
  branching 131, 136, 142, 147
  callianassid burrows 130–132, 137
  comparable assemblages 161
  controls, phobotactic 149
    geotropic 150
  crustacean burrows 130–32, 136–7, 151, 156, 158, 161
  dimensions 132, 134, 136, 140–142
  explanations of 149–158, 160–162
  laminated structures 133*, 138*, 139–141, 155 ; Pl. 1, fig. 4 ; Pl. 5, fig, 1 ; Pl. 8, fig. 3
  patterns of 132, 133*, 134, 135*, 142, 143*, 146*, 147
  Pellets in ; sand 130 ; faecal 130, 137–8
  problematic burrows 158
  scratch marks 151, 153, 155–56
  walls 147, 149, 158
  worm burrows 151, 158, 160
Burrow type A **156** 157*, 158
  type B 157, **158**
  type C **158**, 159*, 160
  type D **160**, 161 ; Pl. 5, fig, 4 ; Pl. 7, figs. 1, 4, 5 ; Pl. 9, fig. 5
  type E **161** ; Pl. 2, fig. 3
Buthrotrephis 148

Calcidelectrix 161
Callianassa major 130, 137
  sp. 131, 162
callianassids 162
  association with trace fossils 131–32
Calymenacea 118
Calymene birmanica 117
Cambarus carolinus 156
Cambrian, Turkey 84, 85
Campophyllidae 208
Cerithium 10
Cephalopoda
  Ammonoidea 1–79
    Collecting techniques 11
    Evolution 64–66
    Homeomorphy 19, 20, 23, 66, 75
    Intersex 54
    Kimmeridgian 11–13
      faunas 4–5, 66–76
    Microconch
      horn 17–18
      lappetts 18
    Palaeoecology 16
    Preservation 11
    Ribs 11–13*, 15, 17
      rib characters 22–23, 25, 32, 38, 40, 51
      rib direction 13
      rib types 13
    Sexual Dimorphism 15–18
Chalk, Lower 125–167
  Bottom conditions 129
  Burrows in 130–34, 137, 140, 142–43, 146, 149, 150, 152–4, 156, 160
  composition of 129
  depth of deposition 129–30
  fauna 161–62
  Mollusca 129
  occurrence 128
  preservation of burrows 131, 137
  sedimentation 128–29
  Trace fossils 154–55, 161
Chandler, M. E. J. 169–179
Cheirurid gen. & sp. indet. 88, **114**, 115 ; Pl. 10, fig. 3
Chondrites **148**–150, 161
  associations 149, 150
  branching 148, 149 ; Pl. 9, fig. 1 ; Pl. 5, fig. 3
  diagnostic features 148
  dimensions 149
  feeding 150
  interpretation 148, 150
  occurrence 149, 150
  patterns 148, 149
  phobotactis 149
  size range 148
  tunnels 149, 150
  walls 149
Chondrites sp. **149**, 150 ; Pl. 2, figs. 2–4 ; Pl. 5, fig. 3 ; Pl. 9, fig. 1
Christianiidae 286, 287
Cladcora antiqua 266
Climacograptus sp. 89, 91, 92
Cliona 161
Clorinda community (Silurian, Lland.) 288, 313
Cocks, L. R. M. 283–324
Codites neocomiensis 161
Coelenterata see also under Phillipsastraeidae
  biometric techiques 199–200
  cerioid corals 194
  Classification 205–208
  Devonian 181–281

Dissepiments
  dissepimental form 184, 207–209, 280
  horseshoe type 184, 190, 198, 205–**206**, 207–209, 281
  in classification 206–208
  peneckielloid 208–209
fan-systems 206–208
Increase
  in colonial Phillipsastraeidae 193–97
  axial increase 193*, **194**, 195–197*, 198
  intercalcinal 193*, **194**
  intermural **194**
  lateral 193*, **194**, 195*, 196*
  thamnophylloid & lateral **195**, 196
  polyp fusion 201–203
massive corals 192–94, 199, 201, 203, 205, 207, 280
microstructure of, 190–93
phaceloid corals 194, 198, 199, 201, 205
plocoid corals 193, 194
pseudocerioid corals 194
Septa
  function 192
  holotheca 193
  microstructure 190, 206
  pseudotheca 192, 196
  septal insertion 193
  septal size 203–4
  variation in septal number 203–4
      septal ratio 203, **204**, 205
      septal size **205**
Standard statistics of, **199**–200
Terminology
  cerioid 192, 194
  plocoid 194
  pseudocerioid 192* 194, 280
Trabeculae
  development of carination 190
  septal trabeculae 206–8
  trabecular fans 206–8
  trabecular structure **190**, 191*
Variation in colonial corals
  average corallite area 199–200
  average tabularium area 199–200
  dimensions 198–9
  general trends 198–204
  septa-tabularium ratio 199, 202, 204
  standard statistics 199–200
  tabularium : corallite area ratio 199–200
  tabularium : corallite diameter ratio 199, 202
  variation in
    diameter **200**, 201–2
    septal number **203**
    septal ratio **203**
    size **201**–203
    tabularium 201
Colpocoryphe 120
  grandis 120
  sp. 85, 88–90, **120** ; Pl. 9, figs. 5, 6, 9, 10
Columnariidae 209

Conodonts, Upper Devonian 189
Coolinia 313
COPE, J. C. W. 1–79
Corals, see Coelenterata
Corophioides 150
CRETACEOUS
  Germany 132, 158
  Great Britain, Southern England 125–167
    Chalk Marl 130
    Glauconitic Marl 128, 140, 149, 152–3
    Lower Chalk see under Chalk
    Paradoxia Bed, trace fossils 142, 144–47
    Plenus Marls, burrows in, 128, 154–5
    Red Chalk 144–5, 147
    Totternhoe Stone 128–9, 137, 140–1, 149–50, 152
    Weald Clay 151
  Tempskya 171, 177
  Trace fossils 125–167
CRUSTACEA
  brachyurous crustaceans 162
  callianassid burrows 130–23, 137
  callianassids 162
  crustacean borings 156
  crustacean burrows 136–7, 151, 156, 158, 161
  decapod burrows 156
  feeding traces 139, 155
  fossil crustacea 162
  fossil crustacean burrows 129, 151
  laminated structures 139
  Lower Chalk crustacea 161–2
  macrurous crustaceans 162
  scratch marks 151, 153, 155
Cruziana 153
Cryptolithinae 95, 97
Cryptolithus 92, 95–6, 102, 107
  cf. *inopinatus* 108
  tesselatus 95
? *Cryptolithus* **bedinanensis** 88, 101, **104**, 105–9; Pl. 3, figs, 1–7, 9 ; Pl. 4, figs. 2–9
  cf. *bedinanensis* 107
  inferus 88, 101, **102**, 103–4, 108 ; Pl. 2, figs. 6–8
  cf. *inferus* 88, 102–3 ; Pl. 2, figs. 2, 4, 7, 12
  sp. Pl. 2, fig. 10 ; Pl. 3, fig. 8
'*Cryptolithus*' sp. 108
Cyathophyllidae 208
Cyathophyllum ananas 228, 247, 249, 253
  caespitosum 266
  caespitosum trigemme 260
  minus 273
  pentagonum 231, 233, 236
Cylindrites 136
  rimosus 161
Cylindrites saxonicus 134
  spongioides 134, 136–37, 145, 158
  suevicus 140
Cyphomena 299, 301, 311, **315**, 316–19
  angulata 316
  (*Laevicyphomena*) **317**

feliciter 288, **317**, 318 ; Pl. 12, figs. 13–14 ; Pl. 13, figs. 1–9
Cyphomenoidea **316**, 321
(*Cyphomenoidea*) *wisgoriensis* 288, 315, **316**, 317–18 ; Pl. 12, figs. 9–12
CZECHOSLOVAKIA
Correlation with Ordovician, Bohemian faunas 91–2, 95, 108–9
Stratigraphy 91–2
Trilobita 109, 112, 114

Dadas Formation, Turkey 88
Dalmanitidae 112
Dalmanitina 86, 88, 90, 112, 113
proaeva cilinensis 112
grandis 112
proaeva 88, 91, **112**, 113 ; Pl. 6, figs. 1–9, 11–13 ; Pl. 7, figs. 4–5
socialis 112–13
davidsoniaceans 319
DEAN, W. T. 81–123
DEVON
Devonian localities 185, 186*, 187–8
Fossil coelenterates 181–281
DEVONIAN
Fossil coelenterates/corals 181–281
variation in 198–204
Great Britain
Devonian 185, 187
Middle 188
Upper 189
Localities 185, 186*, 187
Frasnian 189
fossil markers 188
cordatum Zone 189
holzapfeli Zone 189
lunulicostata Zone 189
Givetian
Middle 185–7
Upper 188
Diaulax 162
Dicoelosia cf. alticavatus 313
Dictyoporus 161
Dionide 109, 111–112
asiatica 112
atra 112
Dionide euglypta var. *quadrata* 112
formosa 91, 109, 110
anatolica 90–1, **109**, 110–12 ; Pl. 5, figs. 1–4 6, 7, 12
formosa 11–12
hybride 112
jubata 110, 112
turbulli 112
Dionididae 109
Diphyphyllum minus 261, 272
Diplograptus sp. 89, 92
Discina latissima 7–10
Discosphinctes 24
Disphyllidae 205–209
disphyllids 207–8
Disphyllinae 206
Disphyllum 205, 208, 258, 271
Disphyllum (*Phacellophyllum*) 257
caespitosum 266
DORSET
Upper Kimmeridge Clay ammonites 1–79
Dorsoplanitinae 63
Dyers Quarry, Devon (Middle Devonian) **185** 186*, 198
Dysidea 150

ECHINODERMATA
Kimmeridgian, crinoid 10
ENGLAND
Devonian corals 181–281
Devonian localities, Devon 185–187
Dorset, Kimmeridgian ammonites 1–79
Upper Kimmeridge Clay 70–71
Lower Chalk, trace fossils 125–167
Silurian, brachiopods 288–315
Enoploclytia 129, 162
EOCENE
Trace fossils
Australia 132
France 151
Great Britain 158
Eocelia 286
Eocelia community (Silurian, Llandovery) 288
Eohomalonotidae 118
Eoplectodonta 321
millinensis 313
Eospirifer sp. 313
Erismatilithus Madreporites radiatus 212
Erodophyllinae 206
Exogyra virgula 9, 10, 69

Fascicularia caespitosa 266
Favastraea intercellulosa 214
Felixium 150–51
Filuroda 161
Foliomenidae 286, 287
FRANCE
Trace fossils, Eocene 151
Upper Kimmeridgian, Boulonnais 72–73
Frechastraea 192, 195, 201, 203, 209, 213, 230, **231**, 232–57
bowerbanki 189, 192, 195, 201, 202, 240, 246–47, **253**, 254–57 ; Pl. 11, fig. 3 ; Pl. 12, figs. 1–3
carinata 189–91*, 192, 195, 202, 241, **242**, 243–47 ; Pl. 9, figs. 1–3
goldfussi 189, 192*, 193*, 195*, 201–203, 246, **247**, 248–253, 280 ; Pl. 10, figs. 1–5 ; Pl. 11, figs. 1–2
micrommata 193, 195, **240**, 241–42 ; Pl. 8, figs. 4, 5
pentagona 280
minima 189, 193*, 195*, 202, **236**, 237–40, 245–47, 257, 281, Pl. 8, figs. 1–3

  pentagona 189, 191*, 192, 195* 202, **233**, 234*–36, 240, 245–47, 253, 281 ; Pl. 6, fig. 5 ; Pl. 7, figs. 1–5
Fucoides targionii 148
fucoids 132, 136, 151, 161
Furcitella 294
Furcitellinae, (Strophomenidae) 286, 288, 293, 294

geotropic control, Trace fossils 150
GERMANY
  Southern (Franconia)
    Upper Kimmeridgian 73–75
    Tithonian 5, 73–75
  Trace fossils 132, 134, 140, 151, 156, 158, 161
Glauconitic Marl, burrows in 128, 140, 149, 152, 153
Glyphea willeti 162
Glyptomeninae 286
GRAPTOLITES
  Turkey, Ordovician 92
Gravesia 23, 66, 68, 72, 75
  cf. *gravesiana* 9, **14** ; Pl. 1, fig. 2
  gravesiana 14, 66, 68–69
  gigas 9, **12***, 14, 68 ; Pl. 1, fig. 1
  irius 14, 66, 68
GREAT BRITAIN
  Devonian 185–187
  Devonian corals 181–281
  Lower Chalk, trace fossils 125–167
  Silurian Brachiopoda 283–324
GREENLAND
  Upper Kimmeridgian 73
Gunnarella 289
Gyrolithes 132, 137, 150
  dewalquei 161

Halymenites cylindricus 136
Haplothecia 207, 213
  filata 213
  ogwellensis 189
  pengellyi 187–88, 201
Heliophyllum cf. limitatum 248
  troscheli 228
Hexagonaria 205–206, 231–32
  firthi 192*
  hexagona 232
Holtedahlina 288
  parva 291
Houghton Regis, (Cenomanian) trace fossil locality 127, 133, 137, 149, 152
Hunstanton, Cretaceous trace fossils 128, 143–6, 157
Hypothyridina procuboides 188

Ichnology, see Trace fossils 125–167
Ichthyosaurus 8, 10
Ilovaiskya 75
Inoceramus 129
  expansus 8, 11
IRAQ
  Ordovician, Sinat Shales 91

JURASSIC
  Ammonites, Dorset 1–79
  Stratigraphy, Kimmeridgian 1–79
    see also under Kimmeridge Clay
  Trace fossils 132, 135, 161

Katastrophomena 288, 291, **293**, 294–98
  penkillensis 288, 291, 294, 296, **297**, 298 ; Pl. 4, figs. 1–6
  scotica 288, 294, **296**, 297 ; Pl. 3, figs. 3–9
  woodlandensis 288, 294, **295**, 296, 298 ; Pl. 2, figs. 1–10
  woodlandensis geniculata 294, 296 ; Pl. 3, figs. 1 & 2
  sp. 298–99 ; Pl. 4, figs. 7 & 8
Keckia ? sp. 131, **155**
KENNEDY, W. J. 125–167
Keratinites **21**, 59
  cornutifer 62
  keratophorus 21
  naso 62
  nasutus 62
? *Keriophylloides* 209, 211
Kimmeridge Clay 1–79
  Blackstone 8, 18, 19, 21
  Cattle Ledge Shales 9, 68–9, 71
  Grey Ledge Stone Band 9, 68, 69
  Hen Cliff Shales 9, 71
  Kimmeridge Oil Shale—see Blackstone
  Rope Lake Head Stone 9, 69
  Yellow Ledge Stone Band 9, 66, 68
  Upper Kimmeridge Clay 1–79
    Ammonite faunas 66–76
    Blake's bed numbers 7–10
    East Greenland 73
    France 72–73
    Germany 73–75
    Great Britain 70–72
    Kimmeridge-Portlandian boundary 75
    Russia 75–76
    Zones 66–70
Kimmeridgian 1–79
  Lower 4
  Upper 1–79
    elegans Zone 64–5, 72–3
    hudlestoni Zone 65, 73
    pectinatus Zone 18, 65, 73
    scitulus Zone 65, 68, 72–3
    virgatites Zone 72
    wheatleyensis Zone 47, 65, 69, 73
  Zones 4–5, 7–10, 66–70
    Aulacostephanus Zone 67–8, 72–3
      Aulacostephanus autisiodorensis Zone 7

Gravesia spp. Zones 67–8, 72
Gravesia gigas Zone 67–8
gravesiana Zone 67–8
irius Zone 67
Pectinatites pectinatus Zone 67
Pectinatites (Arkellites) hudlestoni Zone 8, 67, **69**–71*
(Pectinatites) pectinatus Zone 7, 67, **70**, 71*
(Virgatosphinctoides) elegans Zone 9–10, **66**, 67, 71
scitulus Zone 9, 67, **68**, 71*
wheatleyensis Zone 8–9, 67, **69**, 71
Perisphinctes pallasianus Zone 18, 67, 70
Subplanites grandis Zone 67
? vimineus Zone 67, 69
wheatleyensis Zone 67
Virgatites miatschkovensis Zone 18, 67, 69
nodiferus Zone 67
wheatleyensis Zone 67, 69
Kloucekia 86, 88, 90, 113
phillipsii 91, 113, 114
phillipsii **euroa** 91, **113**, 114 ; Pl. 6, fig. 10 ; Pl. 7, figs. 1–3, 6, 7, 9, 12

Laevicyphomena 316, **317**
Lasiograptus 89, 91
Lennea 160
Lepidocoleus 89, 92
Lepidotus 10
Leptaena 287, **299**, 300–302*, 304–305, 307, 310–11, 315
Associations 301, 308, 313
Distribution and ecology 299, 301, 305, 313
Groups in British Llandovery 301, 302, 310
Ordovician and Silurian spp. 300–301
Relationships 301, 302, 310, 313
Leptaena acuteplicata 301, 302
bella 301
centervillensis 301
contermina 288, 301, 302, **306**, 307 ; Pl 6, figs. 8–13 ; Pl. 7, figs 1–11
delicata 301
depressa 315
var. *vulgaris* 300
elongata 300, 305
haverfordensis 288, 300, 302–3, **304**, 305, 307 ; Pl. 5, figs. 4–15
var. *contracta* 300, 304, 305
homostriata 315
julia 301
loveni 289, 301
martini 302, 303
martinensis 288, **302**, 303, 304 ; Pl. 4, figs. 9–13 ; Pl. 5, figs. 1–3
oklahomensis 301
parvula 289, 301
purpurea 288, 302, **313**, 314, 315; Pl. 12, figs. 1–6
cf. *purpurea* Pl. 12, fig. 6
quadrata 288, 291, 300, 302, 307, **312**, 313, 314 ; Pl. 11, figs. 6–10
quadrilatera 300
reedi 288, 301, 302, 308, **310**, 311 ; Pl. 10, figs. 1–14
rhomboidalis 299
var. *β* 300
var. *γ* 300
var. *δ* 300, 309
var. *ε* 300, 307, 310
var. *ζ* 309
var. *nana* 300
richmondensis 300
var. *precursor* 300
rugosa 299, 300
salopiensis 287
schmidti 300
sinuosus 289, 301
? *tennesseensis* 301
tenuistriata 300
urbana 300, 302, **305**, 306–7 ; Pl. 6, figs. 6, 7
valentia 288, 300–302, **307**, 308, 310–11 ; Pl. 8, figs. 1–8
mullochensis 300, 302, 305, 308, **309** ; Pl. 8, figs. 9–15
valida 288, 300, 302, **305**, 307 ; Pl. 6, figs. 1–5
Leptaena wisgoriensis 301, 316
zeta 288, 300, 301, 302, **309**, 310 ; Pl. 9, figs. 1–6
ziegleri 288, 301–2, **311**, 312 ; Pl. 11, figs. 1–5
sp. **314**, 315 ; Pl. 12, figs. 7–8
sp. (large Woolhope Limestone specimens) 310, 315
? *Leptaena lewisii* 289
Leptaenidae 286–7, 289
leptaenids 286–7, 289, 299, 301, 314, 319
Leptaeninae, (Strophomenidae) 287–89, 294, **299**
leptaeninid 319, 321
Leptaenisca 287
Leptaenoidea 287
Leptaenoideinae 286, 287
Leptagonia 300
Lingula sp. 8, 9
ovalis 8, 9, 10, 69
Lithacoceras 5, **19**, 23–4, 72, 75
Lithodendron caespitosum 258, 259, 266
Lithostrotion 211–2
antiquum 266
hennahi 214
cf. *portlocki* 194
Lloydolithus 108
Lucina miniscula 8–10
Luhaia 287
Lummaton Hill, Middle Devonian, Devon **186**, 187, 201
Lummaton Shell Bed 187–8

Macgeea 206, 209, 258–60, 268
Macgeea (*Macgeea*) 258–60
caespitosa 266
Macgeea (*Thamnophyllum*) 257–60, 271
caespitosa 266

var. *minus* 261. 263
caespitosum 266
var. *minus* 263
minima 261, 263
trigemina trigemina 260
Macgeeidae 207, 209
Macgeeinae 207
Mackerrovia 299, **319**
lobatus 288, **319**, 320–21 ; Pl. 13, figs. 10–15 ; Pl. 14, figs 1–8
macroconchs, Ammonoidea see under Sexual dimorphism
Madrepora ananas 212
Marisastridae 208
Marisastrum 232
Marrolithus anomalis 95
Marrolithoides 90, 92, **95**, 96, 101
arcuatus 101
laticirrus 88, **99**, 100–1, 109 ; Pl. 2, figs. 1, 3, 5, 9, 11, 13
orthogonus 91, **96**, 97–101 ; Pl. 1, figs. 1–9
simplex 101
sp. 88, **101**, 102 ; Pl. 4, fig. 10
Marrolithus 95, 101
Medusaephyllum 209, 211
Megaphyllum 206
microconchs, Ammonoidea refer to Sexual dimorphism
Microtrypa 294
MIOCENE, trace fossils
Austria 131
Borneo 137
Spain 150–51
Modiola autissiodorensis 9
MOLLUSCA
Kimmeridgian, Great Britain 10
Ordovician, Turkey 92

Necrocarcinus 162
Neocampophyllidae 206
Neocolumnaria 206
Neocolumnariidae 206, 208
Neseuretinus 115
Neseuretus 115, 117, 118
birmanicus 117
Neseuretus (*Neseuretus*) 92, 117
birmanicus 92, 117–118
turcicus 85, 88, 91, **115**, 116–7 ; Pl. 7, figs. 8, 10, 11 ; Pl. 9, figs. 1–4

Oepikinae 286
Onnia 108
ornatus 109
Ophiomorpha 136–7, 151, 161
nodosa 136
Opthalmosaurus sp. 9, 10
ORDOVICIAN
Brachiopoda 299–300, 315, 321
Caradoc Series 88, 91–2, 315
Faunas 91–2
Anglo-Welsh 92
Bohemian affinities 91–5, 108–9
Encrinurella fauna 92
Tethyan 92
Llandeilo 91–2, 107
Llanvirn 92, 107
North America, Brachiopoda 315, 321
Stratigraphy 92
Trilobita 91–2
Turkey 83–4, **85**, 86–90
Orionastraea 212
Orthis antiquata 293
scabrosa 293
Ostrea bononinae 7–9, 11
multiformis 8–10
solitaria 7, 11
Oxford area, Upper Kimmeridge 70, 71*, 72
oysters 16

Pachyphyllinae 206
Pachyphyllum 205–7, 209, 211, 213–14, 280–81
bouchardi 214, 281
devoniense 226, 228
? *Pachyphyllum bowerbanki* 254
PALAEOBOTANY
Ferns, *Tempskya* 169–179
PALAEOECOLOGY
Ammonoidea, Kimmeridge 16
Devonian, Corals
environment 185
growth position 198
influences on variation in Phillipsastraeidae 201
Lower Chalk
bottom conditions 129
burrows 130–150
fauna 161–62
trace fossils 130–32, 137, 150, 153
Oysters 16
Silurian Strophomenacea (Brachiopoda) 288–301
PALAEONTOLOGY see under separate Phylla
Collecting techniques 11
Paradoxica Bed, trace fossils 142, 144–47
Parallelodon 11
Paravirgatites 63–4
kimmeridgensis 64
paravirgatus 63
Pavlovia 63, 70, 75
(*Paravirgatites*) 63
paravirgatus 7
cf. *paravirgatus* **63**, 64
' pavlovids ' 22
Pectinatites **14**, 15–18, **19**, 20–24, 39, 60, 64–66, 68, 75–6
Evolution of 64–66, 68
Interpretation of **18**
Origin of **22**–24

Pectinatites aulacophorus 60–61
  pectinatus 21, 63
Pectinatites (*Arkellites*) 8, 9, 18, 24, 68
  cuddlensis 9, 25, **26**, 27–29, 37, 65, 68 ; Pl. 4; Pl. 5, fig.1
  damoni 9, 25, **28**, 29, 65 ; Pl. 5, figs. 2, 3 ; Pl. 6
  hudlestoni 8, 24, 25, **29**, 30, 64, 65, 69, 70 ; Pl. 2, fig. 3 ; Pl. 7 ; Pl. 8, fig. 2
  primitivus 9, **24**, **25***, 26, 28–9, 33, 64–5, 68 ; Pl. 2, figs. 1, 2 ; Pl. 3
  cf. *primitivus* 10
  sp. indet. 7
Pectinatites (*Pectinatites*) 18, **59**, 60, 66
  cornutifer 7, **62**, 63, 65, 70 ; Pl. 25, fig. 3 ; Pl. 26, fig. 2
  eastlecottensis 7, **60**, 61, 65, 70 ; Pl. 26, fig. 1
  cf. *eastlecottensis* 7
  groenlandicus 7, 65 ; Pl. 31
  cf. *groenlandicus* **61**, 62
  inconsuetus 7, 19, **59**, 60, 65, 75 ; Pl. 30
  naso 7, **62**, 63, 65, 70 ; Pl. 32
  proboscide 72
Pectinatites (*Keratinites*?) *groenlandicus* 61
Pectinatites (*Virgatosphinctoides*) 18, 65, 66
  abbreviatus 8, 40, **54**, 55, 65 ; Pl. 26, fig. 3
  clavelli 9, **39**, 40–1, 65, 69 ; Pl. 14
  decorosus 9, 32, **36**, 37, 65 ; Pl. 12
  donovani 8, 51, **55**, 56, 64–5, 70 ; Pl. 25, figs. 1 & 2
  elegans 9, **31**, 32–34, 64–6, 68 ; Pl. 8, figs. 1a, 1b ; Pl. 9
  elegans corniger 9, **33**, 34, 36, 64–5, 68 ; Pl. 10
  encombens 8, 40, **57**, 58–59, 65–6, 70 ; Pl. 27, fig. 1 ; Pl. 28
  grandis 8. 9. 38, **44**, 45, 65, 69, 75 ; Pl. 15, fig. 3; Pl. 18
  grandis acceleratus 8, **45**, 65 ; Pl. 19
  laticostatus 8–9, 38, **43**, 44, 65, 69 ; Pl. 16
  magnimasculus 8, 40, **56**, 57, 65, 70 ; Pl. 29
  major 9, **37**, 38–9, 65 ; Pl. 13
  cf. *major* 9
  pseudoscruposus 19, 38, **49**, 50, 65, 69 ; Pl. 17
  cf. *pseudoscruposus* 8
  reisiformis 8, **50**, 51–2, 54, 59, 65, 69 75 ; Pl. 23, fig. 3
  cf. *reisiformis* 8, 51
  reisiformis **densicostatus** 8, **53**, 65 ; Pl. 23, figs. 1, 2 ; Pl. 24, fig. 2
  scitulus 9, 32, **34**, 35–37, 41, 65, 69 ; Pl. 11
  cf. *scitulus* 9
  smedmorensis 9, 40, **41**, 42, 65, 69 ; Pl. 15, figs. 1 & 2
  wheatleyensis 8, 40, **46**, 47–49, 52, 56, 65, 69 ; Pl. 21
  wheatleyensis delicatulus 8, **48**, 49, 61, 65, 69 ; Pl. 27, fig. 2
  wheatleyensis **minor** 9, **47**, 48, 55, 65 ; Pl. 24, fig. 1
  woodwardi 8, 32, 43, **45**, 46, 64, 65, 69 ; Pl. 20
Pectiniformites 20, 21
  bivius 20
? *Pectiniformites* 59
Peneckiella 189, 191, 206, 209–10, **271**, 272–3
  achanaiensis 274
  boreensis 275
  lateseptata 273, 274
  mesa 273, 275
  minor 272, 273
  minor kunthi 273, 275
  minor minor 274–5 ; Pl. 17, figs. 4 & 5
  nalivkini 274
  salternensis 190, 193–96, 201–2, 269–70, **273**, 274–75 ; Pl. 18, figs. 1–4
Peneckiellidae 206, 208
Peneckiellinae 207
Pentamerus community (Silurian, Llandovery) 288
Pentlandina 288, **289**, 291, 294, 301, 316
  loveni 316
  parva 288, **291**, 293, 313 ; Pl. 1, figs. 7, 8
  cf. *parva* 291
  parabola 288, 289, 291, **292**, 293 ; Pl. 1, figs. 9–12
  tartana 288, **289**, 290–91, 293 ; Pl. 1, figs. 1–6
  sp. **293** ; Pl. 1, fig. 13
Perisphinctidae 12
Perisphinctes eastlecottensis 60
Pexiphyllidae 208
Pexiphyllum 209
Phacelophyllum 257
Phacellophyllidae 209
Phacellophyllinae 206, 207
Phacellophyllum 257–60, 272
Phacellophyllum caespitosum 258, 266
Phacellophyllum (*Phacellophyllum*) 257, 271
Phacellophyllum (*Thamnophyllum*) 257
Phacops phillipsii 114
  proaevus 112
Phillipsastraea bowerbanki 236, 240, 254, 257
  goldfussi 248
  limitata 248
  pentagona 233, 248, 253
  pentagona var. *micrommata* 189, 240, 242
    var. *minima* 231, 236
  sanctacrucensis 231
Phillipsastraeacea 207
Phillipsastraeidae **190**–205, 280
  classification 184
  colonial 193–97
  increase in, **193**, 194–97
  microstructure of, **190**, 191–93
  phylogenetic relationships 207–9, 232
  systematics of, **205**, 206–209
  variation in, **198**, 199–205
phillipsastraeids 280
Phillipsastraeinae 207
Phillipsastrea 184, 191, 195, 203, 205–11, **212**, 213–21, 227–32, 280–1

  ananas 189, 195, 213, **228**, 229, 231, 248, 253 ; Pl. 5, figs. 1–4
  bouchardi 227
  cantabrica 214
  chenouensis 213
  devoniensis 186, 195, 213, **226**, 227–29 ; Pl. 4, figs 1–4
  hennahi 187–8, 207, 213–15, 224–25, 227, 229, 232, 280–81
  hennahi hennahi 187–8, 191*, 192* 195, 201, 202, **214**, 215–21, 224–26, 229, 281 ; Pl. 1, figs. 1–6 ; Pl. 2, figs. 1–4
  hennahi **ussheri** 189, 195, 202, 205, **221**, 222*–25*, 226, 229, 281 ; Pl. 3, figs. 1–3
  hennahii 214, 215
  ibergensis 213, 227, 228
  macrommata 229, 231
  pentagona var. *micrommata* 240–43
  pentagona 233, 240, 248
  radiata 206
  rozkowskae 189, 195, 229, **230**, 231–32 ; Pl. 6, figs. 1–4
  smithi 231
' *Phillipsastrea cantabrica* ' 220
  pentagona 194
Phillipsastrea (*Pachyphyllum*) 211
  devoniense 226
phobotactic behaviour 149
Pholeus 156
  abomasiformis 156
PISCES, Kimmeridgian 10
Placoparina 115
Platycoryphe 120
  ? sp. 88, **120** ; Pl. 8, fig. 4
Plumites sp. 89, 91, 92
Plenus Marls 128, 154, 155
  burrows in Pl. 5, fig. 4 ; Pl. 6, fig. 2 ; Pl. 7, fig. 3
POLAND
  Coelenterates, Devonian 203–4
POLYCHAETES
  tube systems 158
PORTLANDIAN 74
Prismatophyllum 205, 231
  pentagona 231, 233
  prisma 232
Problematicum sp. 154
Producta depressa 300
Protocallianassa 132
  antiquua 137
Protocardia morinica 7–10
Protomacgeea 209
Pseudoacervularia 209, 211, 213
  ananas 228
  roemeri 215
Pseudobilobite 153
Pseudobilobites **153**, 154–5
" *Pseudobilobites* " 153
Pseudobilobites **jefferiesi** 153, **154**, 155 ; Pl. 6, fig. 1 ; Pl. 7, fig. 3 ; Pl. 8, fig. 4 ; Pl. 9, figs, 3, 4, 6
Pseudovirgatites **19**, 20, 23 60, 75
Pseudoblothrophyllum helderbergium 205

Rafinesquinidae 287
Rafinesquininae 286
Ramsleigh Quarry, Devon (Upper Devonian) 186*, **188**, 189, 201
Raphiophoridae 93
Red Chalk, trace fossils 144–45, 147
Redonia sp. 91–2
REPTILIA, Kimmeridge 10
Rhizocorallium 150–51, 161
  glaseli 151
  gläseli 151
" *Rhynchonella* " *cuboides* 188
Ribeiria sp, 89, 91–2
Rogerella 161

Saccoma 8, 10
Saltern Cove, Devon (Upper Devonian) 186*, **189**
Schizocrania sp. 89
Schluteria 206
scratch marks 151, 153, 155, 156
SCRUTTON, C. T. 181–281
Sedimentation
  Lower Chalk 128–9
Selenopeltis 121
  buchi 91, 121
  inermis 121
  inermis **angusticeps** 86, 91, **121** ; Pl. 10, figs. 1, 4, 6, 7, 8
  inermis inermis 91, 121
Sexual dimorphism, Cephalopoda
  criteria 15
  evidence 16–17
  reasons 17–18
  terminology 15
Shaleria 319
Sheppey, Kent (Eocene) 171, 178
Shropshire
  Silurian, Brachiopoda 288–298, 301, 307, 314–5
SILURIAN
  Brachiopoda 283–324
    Great Britain
      communities 288, 313
      Llandovery 286, 288, 291, 293–4, 298–302* 305, 310, 316, 321
      strophomenids 311
      Wenlock 286, 307
  Trilobita 304
Sinuites (s.l.) sp. 89, 91–2
  paradoxica 145, 147
Siphonia pyriformis 145
  tulipa 144–5
Siphonophrentis variabilis 205
Smithia 209, 211, 231
  bowerbanki 231, 253, 254, 257
  hennahii 214, 215
  micrommata 231, 240–43
? *Smithia boloniensis* 231

Sosink Formation **89**, 90
Spain
  Trace fossils, Miocene 150
    Palaeozoic 153
Sphinctoceras **22**, 69
  crassum 22
' Sponges ' 131–2, 136, 150–2, 161
Spongelia 150
Spongeliomorpha 141, 147, **150**, 151, 156, 161
  associations 151
  branching patterns 151
  feeding 153
  internal structure 153
  interpretations 150–53
  occurrence 150–151
  ornamentation 151, 153
  outer surfaces 151, 153
  surfaces ridges 151, 153
Spongeliomorpha ? **annulatum 152**, 153, 157* ; Pl. 2, fig. 1 ; Pl. 5, fig. 5
  iberica 150–52
  saportai 151
  sp. **152** ; Pl. 7, fig. 7
' *Spongeliomorpha* ' *iberica* 151
Spongelites 151
Spongia paradoxica 142, 144, 145, 147
  pertusa 132
  sudolica 147, 151
Spongiliomorpha 150
Spongites 132
  gigas 134
  pertusus 132
  saxonocus 134, 135*, 136–7
  suevicus 140
  suevicus quenstedti 140
? *Streptastrea* 209
  longiradiata 215
Stricklandia 286
Stricklandia community (Silurian, Llandovery) 288
Stringophyllum 186
Stropheodonta funiculata 317
stropheodontid 319
Stropheodontidae 286, **287**, 319
' *Strophomena* ' *agrestis* 297
  antiquata 286, 289–91
Strophomena 288–9
  antiquata 295–7
  antiquata var. woodlandensis 293
  arenacea 319
  dura 293
  hirundo 289
  julia 316
  lindstromi 294
  ? *pectenoides* 294
  cf. *penkillensis* 291
  radiireticulata 294
  rhomboidalis 306, 309
  rugata 294
  scotica 294, 296
  scotica var. *alveata* 294, 296–7
  woodlandensis 295
  aff. *woodlandensis* 295
  woodlandensis geniculata 294
Strophomena (*Pentlandina*) 289
  parva 289, 291
  tartana 289
? *Strophomena sibirica* 294
Strophomenacea 283–324
  classification 286, 287
  distinguishing features
    inter area 311
    muscle scars 301, 306, 310–11, 313, 319
    ornament 296, 315–18, 321
    rugae/rugosity 287, 293, 304, 306–7, 309, 315–16
Strophomenidae 286, 287, **288**, 294, 319
Strophomenidina 287
Strophomenidinae 287
strophomenids 286, 311, 315
Strophomeninae 286–89, 294
strophomeninid 316, 319
Strophonella 298
  costatula 294
  penkillensis 297
Subdichotomoceras **22**
  lamplughi 22
Subplanites 5, 18, **20**, 21, 23–4, 75
  moernsheimensis 23
  pseudoscruposus 49
  reisi 23
  rueppellianus 23
  schlosseri 23
  siliceus 75
  (*Virgatosphinctoides*) *wheatleyensis* 46
Sudetia 272–3
Sulcorphyllum 210, 214
Svobodana 88, 90–2
Swindon area, Kimmeridge Clay 70, 71*, 72
Synatophyllum 206–7
Synhomalensis birmanica 117
Synhomalonotidae 115
Syringophyllum 212
  cantabricum 220
  ? *cantabricum* 214–15, 220

Taonurus 151
  ultimus 151
Teichichnus 139
Tempskya 171, 176, 177
  erosa 171, 178
  grandis 171, 173, 177–8
  knowltoni 175
  rossica 174
  superba 173–4, 178
  wesselii 174
  sp. nov. [= Kent Tempskya] 171, 172–79 ; Pls. 1–12
    affinities of, 176–78

    origins of, 177–78
    siliceous preservation 178–9
    structure of ;
      ‘ false ’ stem 172, 174, 176 ; Pl. 1
      leaf gaps 173–5 ; Pls. 5–7, 9
      leaf traces **174**, 175, 178 ; Pls. 1–9
      meristeles 172, 174–5, 178 ; Pls. 4, 7, & 8
      petioles 172 ; Pls. 1 & 2
      ramentae 172–74
      roots 174, 176–7; Pls. 2 & 3
      scales **174** ; Pls. 2 & 7
      steles 172–5 ; Pls. 3, 4, 8, & 10
      stem 172, **173**, 174–8 ; Pls. 5–7, & 9
    tissues
      endodermis 173–4; Pls. 11 & 12
      epidermis Pl. 12
      inner cortex 173, 177 ; Pl. 12
      parenchyma 173–8, Pl. 10
      phloem 173, 176
      sclerenchyma 172–78 ; Pls. 5, 7, 10, 11
      xylem 173, 174, 176, 177 ; Pls. 10 & 11
Tempskyaceae 176
Terebella lewesiensis 155, 160
‘ *Terebella* ’ **155**, 156
  cancellata 131, **155**, 156, 160, 161 ; Pl. 8, figs. 1 & 2
  harefieldensis 131, 156 ; Pl. 7, fig. 2
  lewesiensis 161
terebellids 131
Teredina amphisbaena 129
TERTIARY
  Tempskya 178
  Trace fossils, Miocene 131, 137, 150–51
Thalassinoides **131**, 132, 134, 147, 151, 161, 162
Thalassinoides
  associations 132
  branching 131, 136, 142, 147
  burrows 137–8, 147–8
  diagnostic features 132
  interpretations 136–37, 139–41
  laminated structures 138*, 139,; Pl. 8, fig. 3
  mounds 136
  occurrence 132, 137, 140–41, 144–45, 147
  ornamentation 140–41
  outer surface 136–37, 141, 143
  pellets 137–8
  protuberances 142
  systems 133, 135, 142, 143, 146–47
  tunnels 140–42, 148–9
  ‘ turn-arounds ’ 136–7, 141
  walls 147, 149
Thalassinoides callianassae 131
  ornatus **138**, **141**, 151 ; Pl. 6, fig. 4 ; Pl. 7, fig. 6
  paradoxica **142**, 143*, 144–46*, 147, 151, 158 ; Pl. 3; Pl. 4 ; Pl. 8, fig. 5 ; Pl. **9**, fig. 2
  saxonicus 133*, **134**, 135*, 136–40 ; Pl. 1, fig. 1 ; Pl. 5, figs. 2 & 3 ; Pl. 6, figs. 3 & 4
  suevicus 140
  cf. *suevicus* 140–41 ; Pl. 1, fig. 2
  visurgae 135*, 140
  sp. 133*, 135*, 146*, 157*
Thamnophyllidae 207–8
thamnophyllids 203–4
Thamnophyllum 185, 187, 191, 196, 206, 209, **257**, 258–71, 273
  caespitosum s.l. 186, 193–4, 196, 204, **266**, 267, 270–1 ; Pl. 15, figs. 2–4 ; Pl. 16, figs. 1–2
  caespitosum caespitosum 204, 268, 271
  caespitosum **paucitabulatum** 187, 193, 196*, 201, 202, 204, **267**, 268–71 ; Pl. 15, fig. 1 ; Pl. 16, figs. 3–7 ; Pl. 17, figs. 1–3
  germanicum group 265–6, 271
  germanicum **germanicum** 204, 258, **260**, 261–5
  germanicum kozlowskii 265
  germanicum pajchelae 204, 262, 264–5
  germanicum **schouppei** 185, 193, 196–97*, 198, 201–5, **261**, 262–6 ; Pl. 13, figs. 1–4 ; Pl. 14, figs. 1–4
  germanicum skalense 204, 262, 264–5
  germanicum superius 265
  hornesi 266
  kozlowskii 204, 265
  kozlowskii superius 265
  monozonatum 266
  stachei 258–60
Thamnophyllum superius 204
  cf. *trigeminum* 261
  trigeminum 258, 260–1
  trigeminum trigeminum 260–1
  sp. **271**
Thamnopora 188
Thrissops 9–10
Tithonian, Germany 5, 73–5
Totternhoe Stone, trace fossils 128–9, 137, 140–1, 149–50, 152 ; Pl. 1, fig. 1
TRACE FOSSILS 125–167
  see also under *Chondrites*, *Thalassinoides*, *Spongeliomorpha*, *Pseudobilobites*, *Terebella* Burrows and Borings.
  associations 131–2, 137
  associated with hard grounds 147–8
  Feeding 138, 150, 153, 155
  fossil records, Great Britain 132–34
  Interpretations 136–37, 140, 144, 147–53, 155–6
  Jefferies Collection 131, 154
  Kennedy Collection 131
  Lower Chalk 125–167
  Nomenclature 137
  ornamentation 140–41, 151
  surface traces 130, 155
Trapezophyllum 206, 209, 214
Trematis ? sp. 89
Tretaspis 304
TRILOBITA
  Ordovician 91–2
    Anglo-Welsh faunas 92, 101, 107–8
    Bohemian faunas 91, 95, 108–9
    Turkey 101, 107, 109, 111, 114
  Turkey 83–120

TRIAS
  Trace fossils
    Keuper, Dorset 132
    Muschelkalk, Germany 140, 156
Trigonia pellati 9, 11
Trinucleidae 95
Trinucleus bureaui 101
  goldfussi 109
  ornatus 109
  ultimus 109
Triplesiidina 287
Tryplasma fascicularia 203
' tubulures ' 148
TURKEY 83–120
  Palaeontology
    Brachipoda 88, 90
    Graptolites 92
    Trilobita 91–120
  Stratigraphy
    Cambrian 84–5
    Ordovician 85, 91–2
    Palaeozoic 84
      Bedinan Formation **85**, 86–8, 91
      Dadas Formation 88
      Sosink Formation 89, 90
  S.E. Turkey 84*, 90
    Bedinan 84, **85**, 86*, 87–8
    Derik 85
    Mardin 85
    Sosink 85–6, **89**, 90*, 91–2
    Ziyaret 89–90

Urechis 130, 158
U.S.A.
  Brachiopoda, Ordovician 315, 321
  Tempskya 177
  Wyoming, Upper Cretaceous 171, 177

VERMES
  Annelids 151
  Arenicolites 158
  Chondrites 148–150, 161
  fossil worm burrows 158, 160
  polychaete burrows 158
  Urechis 130, 158
Virgatites 5, **18**
  miatschkovensis 18
  virgatus 18
Virgatosphinctes reisi 20
Virgatosphinctinae 24
Virgatosphinctoides 5, 18, 20, **21**, 22, 26, **30**, 31, 32*, 33–37, 38*, 39, 40*, 41–50, 51*, 52–57, 64, 65*, 66, 70
  grandis 44
  nodiferus 44
  wheatleyensis 21, 30, 46
Vomacispongites 132

Wealden Beds 171, 178
Wedekindella brilonense 188
Wheatleyites **20**, 59
  eastlecottensis 60
  tricostulatus 20
' *Wheatleyites* ' *reductus* 62
Wolborough Quarry, Devon (Mid.-Devonian) **185**, 186*, 188
Woolwich Beds 171, 179

Xenohelix saxonica 137

Yorkshire area, Kimmeridge Clay 72

Zapfella 161
Zaraiskites 75
' *Zoophytes* ' 131

11 SEP 1970
NATURAL HISTORY

PRINTED IN GREAT BRITAIN
BY ADLARD & SON LIMITED
BARTHOLOMEW PRESS, DORKING